HARVARD UNIVERSITY

LIBRARY

OF THE

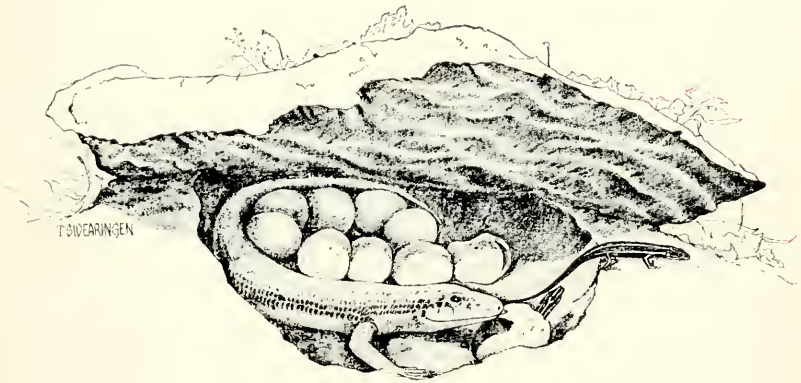
Museum of Comparative Zoology

The Library
Museum of Comparative Zoology
Harvard University

Reproductive Cycles in Lizards and Snakes

MUS. COMP. ZOOL.
LIBRARY
APR 14 1972
HARVARD
UNIVERSITY

Henry S. Fitch



The University of Kansas Museum of Natural History

Institutional libraries interested in publications exchange may obtain this series by addressing the Exchange Librarian, The University of Kansas, Lawrence, Kansas 66044.

Requests of individuals are handled instead by the Museum of Natural History, The University of Kansas, Lawrence, Kansas 66044. When individuals request copies from the Museum the amount indicated below should be included for the purpose of defraying some of the costs of producing, wrapping and mailing. Nos. 6, 12, 17, 27, 36, 37, and 38 are obtainable only from the Arctic Institute.

An asterisk (*) indicates that copies are no longer available from the Museum.

*1. The Museum of Natural History, the University of Kansas. By E. R. Hall and Ann Murray. Pp. 1-16, illustrated. January 5, 1946.

*2. Handbook of amphibians and reptiles of Kansas. By Hobart M. Smith. Pp. 1-336, 233 figures in text. September 12, 1950.

*3. In memoriam, Charles Dean Bunker, 1870-1948. By E. Raymond Hall. Pp. 1-11, 1 figure in text. December 15, 1951.

*4. The University of Kansas, Natural History Reservation. By Henry S. Fitch. Pp. 1-38, 4 plates, 3 figures in text. February 20, 1952.

*5. Prairie chickens of Kansas. By Maurice F. Baker. Pp. 1-68, 4 plates, 15 figures in text. March 10, 1953.

6. The barren ground caribou of Keewatin. By Francis Harper. Pp. 1-163, 28 figures. October 21, 1955. Copies, paper bound, $1.50 postpaid from the Arctic Institute of North America, 1619 New Hampshire Avenue, N. W., Washington, D. C. 20009.

7. Handbook of mammals of Kansas. By E. Raymond Hall. Pp. 1-303, illustrated. December 13, 1955. Paper bound $1.50 postpaid.

*8. Mammals of northern Alaska, on the arctic slope. By James W. Bee and E. Raymond Hall. Pp. 1-309, frontispiece colored, 4 plates, 127 figures in text. March 10, 1956. Paper bound $1.00 postpaid.

9. Handbook of amphibians and reptiles of Kansas. 2nd [revised] edition. By Hobart M. Smith. Pp. 1-356, 253 figures in text. April 20, 1956. Paper bound $1.50 postpaid.

*10. The raccoon in Kansas. By Howard J. Stains. Pp. 1-76, 4 plates, 14 figures in text. July 6, 1956.

*11. The tree squirrels of Kansas. By Robert L. Packard. Pp. 1-67, 2 plates, 10 figures in text. August 20, 1956.

12. The mammals of Keewatin. By Francis Harper. Pp. 1-94, 6 plates, 8 figures in text, 1 map. October 26, 1956. Copies, paper bound, 75 cents postpaid from the Arctic Institute of North America, 1619 New Hampshire Avenue, N. W., Washington, D. C. 20009.

*13. Museum of Natural History . . . University of Kansas. By Roy R. Moore and E. R. Hall. [An unpaged, illustrated "flier," 14½ in. x 8½ in., printed on both sides, and folded twice.] June 1, 1957.

*14. Vernacular names for North American mammals north of Mexico. By E. Raymond Hall, Sydney Anderson, J. Knox Jones, Jr., and Robert L. Packard. Pp. 1-16. June 19, 1957.

*15. The ecology of bobwhites in south-central Kansas. By Thane S. Robinson. Pp. 1-84, 2 plates, 11 figures in text. September 6, 1957.

*16. Natural history of the prairie dog in Kansas. By Ronald E. Smith. Pp. 1-36, 4 plates, 9 figures in text. June 17, 1958.

17. Birds of the Ungava Peninsula. By Francis Harper. Pp. 1-171, 6 plates, 26 figures in text. October 15, 1958. Copies, paper bound, $2.00 postpaid from the Arctic Institute of North America, 1619 New Hampshire Avenue, N. W., Washington, D. C. 20009.

18. Furbearers in Kansas: A guide to trapping. By Howard J. Stains and Rollin H. Baker. Pp. 1-100, 2 plates, 13 figures in text. November 19, 1958. Paper bound 50 cents postpaid.

*19. Natural History Museum. By Roy R. Moore and E. R. Hall. [An unpaged illustrated "flier," 14½ in. x 8½ in., printed on both sides, and folded twice.] May 29, 1959.

20. Handbook of gastropods in Kansas. By A. Byron Leonard. Pp. 1-224, plates 1-11, 87 figures in text. November 2, 1959. Paper bound $1.00 postpaid.

21. Management of channel catfish in Kansas. By Jackson Davis. Pp. 1-56, 8 figures in text. November 2, 1959. Paper bound 50 cents postpaid.

22. Hand-list of the birds of Kansas. By Richard F. Johnston. Pp. 1-6 [folded twice]. May 7, 1960. 10 cents postpaid.

*23. Directory to the bird-life of Kansas. By Richard F. Johnston. Pp. 1-69, 1 figure in text. August 31, 1960.

*24. Natural History Museum. By Roy R. Moore and E. R. Hall. [An unpaged, illustrated "flier," 14½ in. x 8½ in., printed on both sides, and folded twice.] October 19, 1960.

25. Guide to the Panorama of North American Mammals. By E. Raymond Hall, *et al.* Pp. 1-31, silhouettes in black and white of Panorama, life-zones, and taped commentary for each zone. December 15, 1960. Paper bound 50 cents postpaid.

*26. Beaver in Kansas. By F. Robert Henderson. Pp. 1-85, illustrated. December 16, 1960.

27. Land and fresh-water mammals of the Ungava Peninsula. By Francis Harper. Pp. 1-178, plates 1-8, 3 figures in text. August 11, 1961. Paper bound, $2.00 postpaid from the Arctic Institute of North America, 1619 New Hampshire Avenue, N. W., Washington, D. C. 20009.

28. Handbook of unionid mussels in Kansas. By Harold D. Murray and A. Byron Leonard. Pp. 1-184, 45 plates, 42 figures in text. May 10, 1962. Paper bound $1.00 postpaid.

(*Continued on inside back cover*)

Reproductive Cycles of Lizards and Snakes

BY

Henry S. Fitch

MUSEUM OF NATURAL HISTORY
The University of Kansas
1970

UNIVERSITY OF KANSAS
MUSEUM OF NATURAL HISTORY

Miscellaneous Publication No. 52, pp. 1-247, 16 figs.

Published June 19, 1970

Editors:

Frank B. Cross, Philip S. Humphrey, Robert M. Mengel,
and Edward H. Taylor

Lawrence · Kansas

PRINTED BY
THE UNIVERSITY OF KANSAS PRINTING SERVICE
LAWRENCE, KANSAS
1970

CONTENTS

Introduction 1
Procedure 2
Acknowledgments 6
Accounts of Families, Subfamilies, Genera and Species 7
Worm lizards 9
Amphisbaenidae 9
Lizards 10
Gekkonidae 10
Diplodactylinae 10
Eublepharinae 11
Gekkoninae 12
Sphaerodactylinae 20
Iguanidae 22
Agamidae 64
Chamaeleontidae 71
Xantusiidae 74
Scincidae 75
Cordylidae 91
Gerrhosauridae 92
Teiidae 93
Lacertidae 102
Varanidae 107
Anguidae 108
Anniellidae 114
Xenosauridae 115
Helodermatidae 115
Snakes 116
Boidae 116
Typhlopidae 120
Leptotyphlopidae 121
Acrochordidae 122
Uropeltidae 122
Colubridae 122
Colubrinae 123
Natricinae 157
Xenodontinae 172
Dipsadinae 173
Pareatinae 174
Xenoderminae 174
Homalopsinae 174
Sibynophiinae 175
Dasypeltinae 176
Elapidae 176
Hydrophiidae 183
Viperidae 185
Crotalidae 189
Discussion and Conclusions 199
Factors affecting reproductive cycles 199
Size of brood 202
Timing of breeding season 211
Viviparity *versus* oviparity 214
Literature Cited 221

REPRODUCTIVE CYCLES OF LIZARDS AND SNAKES

By
Henry S. Fitch

INTRODUCTION

Every species of animal, in adaptation to its particular ecological niche, has attained various adjustments in the timing of its reproductive efforts and in the numbers of offspring produced. For some years, investigations of the life histories of various reptiles on The University of Kansas Natural History Reservation caused me to become aware of the great diversity of reproductive cycles, even in species occurring in the same environments. Some of these same species were investigated elsewhere in other parts of their geographic ranges, and were found to have somewhat altered reproductive cycles. Interest in reproductive cycles aroused by these findings later led to an investigation of the cycles of several tropical species, and eventually to a general survey of these cycles in the snakes and lizards of the world.

Partly from published literature information has been compiled for many species, but for most of them available data are few. Most detailed life history studies that include intensive investigation of reproductive cycles have been made in the United States, Europe, and Japan, with little information from elsewhere, including the tropics where most species of reptiles occur.

In studying reproductive cycles, I tried to learn as much as possible about the following for each species: 1, Whether it is viviparous or oviparous and, if the latter, whether part of the embryonic development takes place in the female's oviduct; 2, Seasons of copulation, ovulation, oviposition or parturition and hatching—how they are correlated with annual cycles of temperature and precipitation and whether the reproductive cycle is annual, occurs less often, or more often; 3, If more than one brood or litter is produced annually, the length of the interval between ovulation cycles, and the effects of the abundance or scarcity of food; 4, Lengths of incubation or gestation periods; 5, Time required for growth and development from hatching or birth to sexual maturity; 6, Numbers of eggs per clutch or young per litter; 7, Intraspecific differences in

the above factors, arising from innate individual variation, from age and size, and from geographic variation.

Information was accumulated on all of these subjects, but was incomplete for every species. More than 50 species have been the subjects of detailed study, and their reproductive cycles are relatively well known, but for most only meager data or scraps of information are available from which reproductive cycles may be deduced. Even such poorly known species are included, because it is evident that each species is to some extent unique in its reproductive pattern, although trends can be discerned for groups of species, both on the basis of phylogenetic relationship and on the basis of response to a particular type of climate or habitat.

PROCEDURE

Essentially, the data and conclusions presented herein originate from three sources: 1, My field studies of various species of lizards and snakes, chiefly in Kansas, California, and Oregon, but also in most of the states in the far western United States, in Louisiana, in Costa Rica for eight weeks in 1965, and in Ecuador in March of 1967; 2, Study of preserved museum specimens, chiefly in The University of Kansas Museum of Natural History, the University of California Museum of Vertebrate Zoology, The American Museum of Natural History, and the University of Texas Natural History Museum; 3, Survey of published literature.

The personal observations of my collaborators and me have involved the following species: *Agkistrodon contortrix, Agkistrodon piscivorus, Ameiva ameiva, Anolis chrysolepis, Anolis cupreus, Anolis fuscoauratus, Anolis humilis, Anolis lemurinus, Anolis leptoscelis, Anolis limifrons, Anolis lionotus, Basiliscus basiliscus, Basiliscus vittatus, Carphophis vermis, Cnemidophorus deppei, Cnemidophorus exsanguis, Cnemidophorus sexlineatus, Cnemidophorus tigris, Coluber constrictor, Crotaphytus collaris, Crotalus viridis, Ctenosaura similis, Diadophis punctatus, Elaphe obsoleta, Eumeces fasciatus, Eumeces obsoletus, Geophis brachycephalus, Gerrhonotus coeruleus, Gerrhonotus multicarinatus, Gonatodes albogularis, Heterodon nasicus, Heterodon platyrhinos, Holbrookia maculata, Holbrookia texana, Kentropyx calcaratus, Mabuya alliacea, Neusticurus ecpleopus, Ophisaurus attenuatus, Sceloporus jarrovi, Sceloporus malachiticus, Sceloporus occidentalis occidentalis, Sceloporus occidentalis biseriatus, Sceloporus undulatus erythrocheilus, Sceloporus undulatus garmani, Sceloporus undulatus hya-*

cinthinus, Sceloporus variabilis, Sceloporus virgatus, Scincella cherriei, Scincella laterale, Thamnophis elegans, Thamnophis ordinoides, Thamnophis sirtalis, Urosaurus ornatus, and *Uta stansburiana.* Observations on each of these species in its natural surroundings have been supplemented by the examination of substantial museum series. Additionally, sizable museum series of each of the following have been examined to determine reproductive cycles even though I had little or no opportunity to study them under natural conditions: *Ameiva festiva, Ameiva undulata, Anolis tropidolepis, Bothrops atrox, Callisaurus draconoides, Cnemidophorus guttatus, Corytophanes cristatus, Crotaphytus wislizenii, Dipsas catesbyi, Gerrhonotus monticolus, Gerrhonotus moreletii, Imantodes cenchoa, Leimadophis reginae, Lygophis taeniurus, Leptodeira annulata, Oxyrhopus petola, Pseudoboa bitorquata, Sceloporus chrysostictus, Sceloporus clarkii, Sceloporus graciosus, Sceloporus magister, Sceloporus undulatus elongatus, Sceloporus undulatus tristichus,* and *Xenodon severus.*

For the remaining 750 species dealt with, no original information is presented, but condensed accounts of the reproductive cycles, insofar as they can be construed from the literature, are included, or if little information was available, the species concerned are only briefly mentioned in text or tables. There are excellent accounts of the reproductive cycles of a few dozen species that have been the subjects of special study, but these represent only a small percentage of the species that need to be studied, and most of them are limited to the Temperate Zone. No information is available concerning the reproductive cycles of most kinds of reptiles.

Although reproductive cycles have been thoroughly studied in relatively few species of reptiles, an extensive and scattered literature in many languages pertains to hundreds of species in all parts of the World. To find and digest all the literature involved would be a herculean task, perhaps beyond the capacity of one individual. Nevertheless, I have undertaken a general survey of the literature, using more than 600 publications but placing much reliance on comprehensive regional works such as those of Wright and Wright (1957) and Stebbins (1954) for the United States, Pope (1935) for China, Smith (1935, 1943) for India, FitzSimons (1943, 1962) for South Africa, and Fuhn and Vancea (1961) for Romania. Many literature records cited by these authors have been accepted with-

out tracing them to the original publications, which were often inaccessible.

Before the last decade there were few papers dealing primarily with reproductive cycles and many of the records herein cited were gleaned from casual mention of breeding, gravid females, oviposition, or hatching of eggs or birth, in papers whose main emphases were taxonomic or faunal. Herpetologists were so preoccupied with these aspects of their science that they often failed to include the sorts of data pertinent to the present study. Interest in breeding cycles is a relatively recent development. Many published breeding records that would have been of much significance were unusable because the author had neglected to mention the date. A few authors have been commendable exceptions to this lamentable trend. Loveridge in his many technical papers on tropical African reptiles, in both faunal surveys and taxonomic revisions, consistently included notes on natural history, such as breeding condition, and time of appearance of young, so that a wealth of information has accumulated for this part of the World. Similarly, Pope, in his monumental work on the reptiles of China (1935) included a large number of original records of reproduction. He also summarized previous pertinent literature. Minton (1966) in West Pakistan, Anderson (1963) in Iran, Broadley (1959) in southern Rhodesia, and Taylor in Thailand (1963, 1965) likewise provided many valuable ecological notes. Unfortunately most herpetologists in the American tropics have not followed the good examples of these workers, though Stuart's publications on the Central American herpetofauna include many useful notes on natural history.

Some exceptionally significant and useful papers are those of Fukada (1965) on the reproduction of Japanese reptiles, DeHaas (1941) on the breeding of Javanese snakes, Kopstein (1938) on Malayan snakes, Inger and Greenberg (1966) on breeding of lizards in equatorial rain forest, Robertson, Chapman and Chapman (1962, 1964) on Tanganyikan reptiles, and Harris (1964) on the rainbow lizard of Nigeria. Bustard's (1955 to 1969) numerous papers on African and Australian lizards both in captivity and under natural conditions also deserve mention. Important studies of exotic lygosomine skinks are those of Wilhoft (1963, 1965) in the Australian tropics, and Barwick (1959) in New Zealand. In the United States reproductive cycles of reptiles have received much more attention, notably in the intensive studies of Mayhew, Tinkle, Blair, Kennedy, Carpenter, Clark, and Platt. Monographs of the

African geckos by Loveridge (1947) and of the rattlesnakes by Klauber (1956) likewise contain much important information on the reproduction of these groups.

For a few of the species occurring near my family home at Medford, Oregon (1920's and 1930's), or at the San Joaquin Experimental Range in Madera County, central California (1938-1942 and 1945-1947), or at The University of Kansas Natural History Reservation in Douglas County, northeastern Kansas (1948-1967), I have obtained data on reproductive cycles in the course of autecological investigations. Day by day observations on marked individuals throughout the season of their activity, and techniques such as palpation of gravid females to count numbers of eggs or embryos, and cloacal smears to demonstrate recent insemination have been utilized.

Many other species were studied principally from preserved museum specimens. In examining preserved material, the procedure was to determine the reproductive status of each sexually mature female—whether nonfecund, having ovarian or oviducal eggs, or recently parturient—and to measure to the nearest millimeter (snout-vent length) each specimen in a series. The measurements of immature specimens were especially significant in indicating the amount of growth made by each individual since hatching or birth, hence the probable age, and by extrapolation, the time of breeding in the population represented. Specimens of minimum size usually had prominent umbilical scars indicating recent birth or hatching, and with a somewhat wider margin of error, the approximate times of egg-laying and of conception. Growth rates are well known for relatively few kinds and anyhow are subject to much variation between individuals of a species even in one locality. Nevertheless, the size-distribution of young in a population sample often provided good evidence of whether year-round breeding prevailed, or whether the breeding season was long or short. In some instances, even though collection dates were all at one time of year, the young formed a graded series from hatchlings to subadults, whereas in other instances young formed one or more discrete size groups, indicating concentrated breeding periods, with nonbreeding periods intervening.

Gonads were examined in adult female specimens when the abdomen had already been slit or when it was permissible to make an incision for this purpose. Eggs in such specimens were measured and counted. Testes were sometimes measured in male specimens,

but relatively little attention was devoted to them. My purpose was to relate reproductive cycles to the population dynamics of the species concerned, and in this regard the cycle of the female is more critical than that of the male. When fecund females are present in the population there are usually males available to inseminate them. For example, at The University of Kansas Natural History Reservation I found that male snakes of most species have motile sperm in their vasa deferentia throughout most or all of their active season but that females ovulate only during a brief period in spring. Only in exceptional instances is availability of breeding males thought to be critical. For instance, Mayhew (1966) in his study of the desert iguanid, *Uma*, found that in years with inadequate moisture and food, the male gonads were inhibited and he implied that this was a factor in greatly reducing the number of young produced in dry years. However, in many kinds of snakes and at least some lizards there is prolonged storage of viable sperm in the oviducts, and once a female has mated, the further availability of males may have little effect on her productivity.

Measurements, including those of reptiles themselves and of eggs, are given in millimeters in nearly all instances. Both fractional and decimal figures are used and imply different degrees of precision; ½ indicates measurements in units of one-half, whereas .5 indicates measurement in tenths.

In using literature records I have tried to make the citations as brief and compact as is consistent with clarity. Although avoiding direct quotations in most instances, I have tended to preserve the wording of the original author in order to minimize the chance for unintentional change in meaning.

The manuscript was submitted for publication on May 26, 1967. Subsequently minor revisions were made, and information concerning additional species was incorporated from recent literature.

ACKNOWLEDGMENTS

Special thanks are due to the curators who permitted use of various collections and extended many courtesies during my studies—W. Frank Blair of the University of Texas Natural History Museum, Charles M. Bogert of the American Museum of Natural History, William E. Duellman of the University of Kansas Museum of Natural History and Robert C. Stebbins of the University of California's Museum of Vertebrate Zoology. James A. Oliver of the American Museum of Natural History provided encouragement and directed me to important literature. Philip W. Ogilvie kindly contributed his firsthand observations of various species of reptiles in East Africa. James D.

Rising contributed many reptiles collected in Arizona. W. Charles Kerfoot and Eric Shulenberger (assisted by Dennis and Roy O'Connor), Charles J. Cole, and Laurence M. Hardy made extensive collections for me in the southwestern United States and helped with the museum aspects of the work, as did Howard Freeman and Donald R. Clark, Jr. Roger Conant and Charles E. Shaw contributed records of reproduction of snakes in zoos which were of outstanding interest. My wife, Virginia R. Fitch, and my daughter, Alice V. Fitch, assisted me in the examination of museum specimens; my wife also typed the manuscript, and my daughter assisted with various aspects of the field work, including the checking of live-traps on The University of Kansas Natural History Reservation, and the collecting of specimens in the southwestern United States, in this my son Chester W. Fitch likewise participated.

My co-workers and graduate students, Ray D. Burkett, Donald R. Clark, Jr., Russell J. Hall, William S. Parker, and Dwight R. Platt provided information on the reproductive cycles of several North American lizards and snakes from their own intensive field studies. My son John H. Fitch contributed breeding records of several Pacific island lizards. Daniel Janzen helped by loaning me collecting equipment and contributing specimens. Arthur C. Echternacht contributed breeding records of Central American teiids. Edward H. Taylor and William E. Duellman read the manuscript and made many useful suggestions. John D. Lynch advised me concerning many nomenclatorial problems and contributed original records. The National Science Foundation, Division of Environmental Biology supported this study with a grant G-16104 during the years 1959 to 1962 and supported my field research on ancillary projects with three subsequent grants from 1963 to 1969.

ACCOUNTS OF FAMILIES, SUBFAMILIES, GENERA AND SPECIES

An attempt has been made to maintain a fairly uniform system of presentation. Brief general statements for each family and genus include mode of reproduction and trend of reproductive cycles, the geographic area of occurrence and important characteristics of the group, especially those directly concerned with method of reproduction. Such information is, of course, available in greater detail in the literature, but the groups here included are seldom dealt with under one cover, and most herpetologists have little familiarity with the reptile fauna outside of one or two continents. Separate species accounts are included for most groups, but not for certain families like the Amphisbaenidae, Anniellidae, Dibamidae, Hydrophiidae, or Xenosauridae, nor for numerous genera, for which detailed records for species were meager. In general, subspecies have not been dealt with or even mentioned in the species accounts except that in occasional instances where intraspecific differences have been noted or suspected, trinomials have been used as convenient basis for comparing populations. Especially in the large

and ecologically diverse genus *Sceloporus* brief accounts of the several species groups are included, and also separate accounts of several subspecies in instances where notable reproductive differences between populations have been demonstrated.

In comprehensive works on reptiles the sequence in which the various families and subfamilies are treated is not well standardized, but the general trend, with supposedly more primitive groups preceding those that are more advanced, is followed here. Within the families (or subfamilies when these are used) and genera the sequence is alphabetical. I have attempted to use currently acceptable scientific names and often these are different from the ones under which the information was originally published. In some instances, especially for exotic species, I may have inadvertently used outdated or incorrect names.

In the arrangement of families and subfamilies I have tried to reach a satisfactory compromise by using traditional and familiar groupings but at the same time trying to follow systems not too outdated. Subfamilies have been included only for Geckonidae where they represent groups formerly accorded family rank that are notably different in their reproduction, and in the Colubridae where the exceptionally large number of genera need to be broken up into more convenient units. The subfamily Boiginae as widely recognized in the past is not used here, because of the consensus among herpetologists that this is not a natural group, and that the transition from solid teeth to grooved fangs (or vice versa) occurred repeatedly in the evolution of the colubrids. Nevertheless some of the "boigine" genera constitute closely related series, and to avoid dissociating them, all the groove-fanged venomous colubrids formerly included as boigines are retained in a separate alphabetical series following that of the aglyphous colubrines. Except for combining the Boiginae with the Colubrinae, and for ranking the Acrochordidae as a distinct family, I have essentially followed the system of classification for snakes used by Taylor (1965).

Underwood's recent (1967) work has resulted in drastic changes in ideas of relationships within the snakes, and notably in the dismemberment of the family Colubridae as formerly understood. His system has not been followed here. Although it seems to be based on valid data, it is admittedly tentative and subject to further revision so that the more traditional and familiar system is considered more appropriate for my presentation. No systematic judgments are intended by my arrangements. Rather, I have ac-

cepted uncritically arrangements that have been widely used and seem to reflect the thinking of a large number of herpetologists.

Worm Lizards

Amphisbaenidae

Although recent investigations have suggested that the "worm lizards" are not true lizards but constitute a separate suborder of squamate reptiles, Amphisbaenia (Gans, 1967), they are briefly considered here because of their traditional position as a saurian family. However, the genus *Trogonophis* and its near relatives have been placed in a separate family, Trogonophidae.

The worm lizards are fossorial reptiles in which the eyes are reduced or vestigial, the body is elongate and annulated, and the limbs are lacking or else represented only by much reduced forelimbs. The group is mainly tropical but extends into the temperate zones and occurs in Africa and the Mediterranean region, South and Central America, the West Indies, Florida and western Mexico. Loveridge (1941:362, 393, 436) cited several observations of reproduction in the African species. Seemingly most are oviparous, but some (trogonophids only?) are viviparous. A specimen of *Chirindia ewerbecki* taken on April 27, 1939, contained a single remarkably elongate egg (31 × 2 mm). Two females of *Tomuropeltis pistillum* taken at the end of August each contained four eggs which were approximately 35 × 9 and 35 × 10 mm. On September 20 a third individual laid four eggs which measured 26 × 9, 30 × 9, 32 × 8, and 35 × 8 mm.

A pair of Saharan *Trogonophis wiegmanni* were observed intertwined but not copulating on June 10. Another observer found that a female of this species which he had placed in a collecting bag, had given birth to five young. Bons and St. Girons (1963) found that in *T. wiegmanni* spermatogenesis commences in October and is increased in spring, copulation occurs in June, ovulation takes place by the end of June and young are born in September. They found that in *Blanus cinereus*, another Moroccan species which is probably oviparous, the seasonal sequence of spermatogenesis, copulation and ovulation is the same as in *T. wiegmanni*. Adult females do not necessarily reproduce annually, but may go for longer intervals without becoming fecund. Gans (1964:9) reported that a female of *Amphisbaena dubia* from Curitiba, Parana, Brasil, contained three elongate eggs, each encased in a thin leathery shell.

Carr (1949:77) found a clutch of two eggs of *Rhineura floridana* hatching on September 12, 1943 at Gainesville, Florida.

Lizards

Gekkonidae

The geckos constitute a large family of lizards most of which are tropical. Within the tropics they are abundant and widespread; they occur on all the continents (except Antarctica) and throughout Polynesia. They are primitive in various anatomical features, but in other respects they are highly specialized, notably in having the feet and digits modified as scansorial adaptations.

According to Kluge (1967:5): "Some species exhibit no definite seasonal reproductive cycle, and mating may take place throughout the year, but in other forms breeding appears to be cyclic and is restricted to a very short period during the year. There is evidence that some females can retain sperm for a considerable period. . . . In others delayed oviposition occurs until embryonic development is well advanced."

Several distinct families of geckos have been recognized in the past, but Kluge (1967) has included all in the Gekkonidae, and has considered the main groups of geckos to be subfamilies. Besides having trenchant anatomical differences, these subfamilies differ notably in their reproduction.

Diplodactylinae

These geckos constitute a relatively small group of 14 genera in Australia, New Zealand, and New Caledonia. They produce two parchment-shelled eggs per clutch—except for the three New Zealand genera *Heteropholis, Hoplodactylus,* and *Naultinus* which bear living young.

Oedura

Bustard (1967) has studied the reproduction of several species of this Australian genus. He considers the soft parchmentlike eggshells of these lizards to be more primitive than the calcareous eggshells of most other geckos. Despite oviparous habits and soft-shelled eggs the lizards of this genus often occur in extremely arid climates. Bustard's observations led him to conclude that in the relatively cool climate of south Australia one clutch per female per year is the rule, but that in the north a female may produce several clutches in the course of a season. Often a day or more elapses between the laying of the first and the second egg in a clutch. Bustard recorded the following dates

of oviposition for clutches. *Ocdura marmorata:* September 29 and October 1, October 18 (both eggs), October 28 (both eggs), November 9 and 12; *O. castelnaui:* December 23; *O. tryoni:* January 1 (3 clutches); *O. ocellata:* December 31, January 4 (3 clutches), February 12; *O. lesueurii:* September (no specific date) and December 23. Incubation periods noted by Bustard include 60 days for *O. castelnaui*; 49 days (for 5) and 51 days (for 1) for *O. tryoni*; 39 days (for 2) and 43 days for *O. ocellata* and 31 days for *O. lesueureii.*

Eublepharinae

This is a small subfamily of geckos represented in both the Old World (southwest and southeast Asia, Malaya, Borneo, Sumatra, West Africa, Somaliland) and the New World (southwestern United States south to Costa Rica). Taylor (1956:16) stated: "Two eggs are laid." They resemble those of diplodactylines in having soft parchmentlike shells.

Aeluroscalabotes

These geckos are limited to Borneo, Malaya, and adjacent regions of southeastern Asia. They are nocturnal and arboreal and have rather elongate bodies and long legs with short toes that are compressed distally and bear retractile claws. In their study of breeding cycles in equatorial rain-forest lizards of Nanga Tekalit, Borneo, Inger and Greenberg (1966:1015) collected 80 adult female cat geckos, *A. felinus,* of which 32, distributed over 11 months of the year, were gravid each with two eggs.

Coleonyx

The banded geckos are terrestrial, desert lizards of the southwestern United States and the Mexican Plateau and the Pacific lowlands from Colima, México, southward into Costa Rica. The growing season is long in the areas occupied, and dates on which gravid females have been collected indicate that two or more clutches are produced.

Coleonyx brevis.—Werler (1951:37) recorded that two females from San Ygnacio, Texas, both laid eggs at the San Antonio Zoo on April 8, 1950.

Coleonyx elegans.—Alvarez del Toro (1960:74) wrote that in Chiapas, México, this gecko lays a clutch of three or four eggs, but near Chilpancingo, Guerrero, México, on June 11 and July 2, Davis and Dixon (1961:38) found that two females each had two large ova ready to be laid, and in Yucatán, México, Duellman (1965:27) found that females collected on April 9, 1963, and August 15, 1962, also each contained two eggs.

Coleonyx variegatus.—Klauber (1945:142) stated that this species of the southwestern deserts lays two eggs. He mentioned one from San Diego County, California, which contained oviducal eggs on May 25 and another from Los Angeles County which contained oviducal eggs on June 21. As an indication of trend in seasonal activity Klauber listed the following numbers found on roads

in the course of night driving: March, 1; April, 45; May, 340; June, 130; July, 28; August, 24; September, 8; October, 12.

William S. Parker (MS) made a population study of these and other common lizards at Phoenix, Arizona. He found females containing eggs (visible through the ventral body wall) from May through September and found hatchlings from July through November. Therefore he was convinced that individual females produce repeatedly within the same season; probably there are normally three clutches on the average in fully adult individuals. One had large eggs when captured on June 30, and again on July 28. Frequency of gravid females was highest in May and June. It was deduced that incubation lasts about 45 days. Females hatched early in the season grew to adult size by fall or by the following spring. Seemingly, young hatched in September or October grew to maturity by the following late May, June, or July.

Eublepharis

These are terrestrial geckos usually found in dry, rocky places. There are four species, all Asiatic.

Eublepharis macularius.—Anderson (1963:435) mentioned finding females of the fat-tailed gecko in Iran carrying unlaid eggs on April 21, 1958, May 22, 1958, and August 20, 1958. Seemingly egg-laying occurs through much of the season that the lizards are active, and several clutches per female in the course of a season might be expected. Minton (1966:73) observed this species in West Pakistan. A female laid clutches of two eggs each on April 21, May 10-12, and June 8. The eggs in the second and third clutches were fertile, although the female had been isolated from males since April 8. Minton mentioned other females containing eggs in August and September, and noted that most young of the year appear in September and early October. He stated that one female laid a clutch of three eggs.

Geckoninae

The majority of gecko species and genera belong to this subfamily, which is cosmopolitan in the tropics and extends into the Temperate Zones. The eggs are hard-shelled and calcareous. Typically there are two eggs, laid together and glued to the substrate in a sheltered situation, or even in the open, instead of being buried in the soil like most reptilian eggs. Many eggs, up to 186 (M. Smith, 1935:27) may accumulate in a cluster through communal laying. Incubation sometimes requires several months. A few kinds that are relatively small, *Aristelliger* sp., *Gehyra variegata,* are exceptions to the general rule in laying only one egg instead of the usual two.

Cnemaspis

These are small tropical geckos of Africa, Asia and the East Indian Archipelago.

Cnemaspis africanus.—Loveridge (1947:94) published some data on reproduction of this forest gecko: April 22, a gravid female; July 5, female containing an egg with two freshly laid eggs nearby, beneath a log; July 1-7, 12 eggs found; October 31, two eggs laid by a female in British Cameroons; November 22, two eggs found in Uganda and three pairs of eggs found in Kenya; December 12, gravid female; December 21, 31 eggs collected, some newly hatched. Seemingly reproduction occurs throughout the year.

Cnemaspis quattuorseriatus.—Loveridge (1947:88) recorded 12 eggs, one hatching, in the Belgian Congo on March 3, and eggs on November 18 and 21 in Uganda.

Cosymbotus

These tropical geckos often live as household commensals in the Orient and East Indies. Church (1962:262) studied the reproductive cycle of *C. platyurus* in Java. He found that mating is not seasonal, but rather that breeding occurs throughout the year in the equatorial region of his study. Copulation may take place when the eggs are small. There are fecund females in every month. There are no fat bodies. The larger the female lizard, the more likely it is to have ripe or maturing ova.

Cyrtodactylus

This is a large genus of small, somewhat arboreal, Old World geckos.

Cyrtodactylus kachhensis.—Minton (1966:78) found females containing large eggs in West Pakistan in nearly every month. He stated that there are one or two eggs per clutch.

Cyrtodactylus kotschyi.—Loveridge (1947:66) reported eggs found between June 30 and July 7 on Amorgas Island of the Cyclades in the Mediterranean.

Cyrtodactylus malayanus.—In tropical rain forest at Nanga Tekalit, Borneo (1° 37′N), Inger and Greenberg (1966:1010) studied the breeding cycle of this gecko. Males appeared to be in breeding condition all year; likewise there were females with oviducal eggs and others with enlarging ovarian eggs at all times of year, with no distinct seasonal pattern. One female had only a single oviducal egg but each of 35 others had two. In females having oviducal eggs, the ovarian eggs were always minute and whitish. In adults without oviducal eggs, there were always ovarian eggs that were larger and yellowish, obviously growing in preparation for ovulation.

Cyrtodactylus pubisulcus.—This species also was studied by Inger and Greenberg (1966:1010) at Nanga Tekalit, Borneo. As in *C. malayanus,* males showed seasonal fluctuation in reproductive activity. In most months approximately one-fourth of the adult females contained oviducal eggs, but small samples in January, March and June contained none with oviducal eggs, and in both July and August two of three females in the monthly samples were gravid. These deviations probably are not significant, and presumably breeding activity is maintained at about the same level throughout the year. As in *C.*

malayanus, only females that lacked oviducal eggs contained enlarging yellow ovarian eggs.

Cyrtodactylus scaber.—Loveridge (1947:65) reported two sets of eggs found on August 2 at Port Sudan. In Iran, Anderson (1963:437) found hatchlings common in mid-August. A female laid two eggs in late August. A breeding season spanning many weeks is indicated, hence perhaps females have the potential of producing two or more clutches in a season.

Gehyra

These small to medium-sized, nocturnal scansorial geckos occur in Australia and islands of the southwest Pacific. Bustard (1964:269; 1969) studied *G. variegata* in disturbed forest areas of New South Wales, Australia, and found that the lizards do not breed until their third year. "Females lay one egg at a time and normally two ovipositions occur each summer. The first egg is deposited in late November or early December and the second egg in the first or second week of January." Of 103 mature females 96 per cent bred twice, one per cent bred only once and three per cent may not have bred at all. Incubation required three months and survival of eggs was inversely proportioned to the amount of rainfall. The larger, sympatric, *G. australis* was found to lay two eggs per clutch. In the tropical climate of Cape York, Bustard found that the breeding seasons of both species extended into "winter."

Eggs of *G. oceanica* have been noted from October 27 to November 27 (3 clutches) on Rennell Island in the Solomons (Volsoe, 1956:122) and on May 14 and 16 in the northern Marianas (Cagle, 1946b:101).

Gekko

These large, heavy-bodied geckos of India, southeastern Asia, the East Indies and northern Australia live in or about buildings in close association with man, and are scansorial. The tokay, *G. gecko*, is widely distributed in southeastern Asia and the Malayan Archipelago. Smith (1935:112) stated: "The calling is not continued throughout the whole year. It commences about the middle of the cool weather (December), becomes more frequent as hot weather approaches, and is at its maximum during March, April, and May. During these months they can be heard calling frequently, sometimes all through the night, one lizard after another taking up the cry from house to house. After these months they call less frequently, and during the autumn are usually silent." The vocalizations of the tokay seem to be primarily territorial and probably the waxing and waning of territorial vocalization is closely correlated with the breeding cycle in this lizard, as in male birds. There are two eggs per clutch.

Fukada (1965:75) cited the studies of other authors in Japan indicating that the egg-laying season is from June to August, with two eggs per clutch (an instance of three eggs being laid is mentioned), only one clutch per year, and an incubation period of 55 days in *G. japonicus*.

Gymnodactylus

These are small, Neotropical geckos closely related to the Old World *Cyrtodactylus*. In Brasil, Vanzolini (1953:260) reported five clutches of two

eggs each of *G. geckoides* in March of three different years. The eggs were incubated in the laboratory and hatched after intervals of 15 to 170 days; hence, the author concluded that they were laid at different times of year. One female laid her eggs in captivity on February 3, and they hatched after 206 days, on July 18. The clutches of eggs found in the field would have been laid in September, September, October, November, and February, if all had a six to seven month incubation period, as indicated by the one clutch kept from laying to hatching. Presumably in this tropical climate there is some variation in the incubation period depending on the situation and ambient temperature of each egg, but this might be a fairly minor factor.

Hemidactylus

This large genus contains mostly medium-sized species living in the southern parts of Europe, Asia, Polynesia, and tropical America.

Hemidactylus albofasciatus.—Grandison and Soman (1963:324) reported finding of many clutches with two eggs in January in Maharashtra, India.

Hemidactylus brookii.—Loveridge (1947:140) wrote that in November each of four females contained two eggs. In French Equatorial Africa on December 2 a female contained two eggs, and on December 16 a pair of eggs contained advanced embryos. A female from Tanganyika contained two eggs on February 4. Bustard (1957:73) received a group of these lizards from Ceylon in March 1955, and noted copulation twice in that month. Eggs were laid in early May, on July 17, August 21 and August 27. Incubation lasted for two and one-half months. Seemingly breeding occurs at various times of year. Bustard's observations indicate that a female takes interest in her newly laid eggs and attempts to cover them with moss or other material; females in the process of regenerating broken tails will not mate. Minton (1966:83) found that in West Pakistan egg-laying of the spotted house gecko seems to be almost continuous from March to October, but it is not known how many clutches are laid by a single female.

Hemidactylus flaviviridis.—At Delhi in northern India, Sanyal and Prasad (1967:627-633) used a sample of 374 specimens in a year-round study of this house gecko. At this locality, outside the tropics, there is a short annual breeding season in March and early April. Eggs are laid in late April and early May. Gonads of both sexes are of minimum size and in a quiescent state during June and July, and pass into a recrudescent phase in late summer and autumn. The males have spermatozoa in the vasa deferentia from October to May. There is a gradual development of large yolk-laden follicles that reach their maximum size in April in the females. Young hatched in May and June grow rapidly and attain adult size of about 50 mm snout-vent length in August or September. The eggs require 36 to 39 days for incubation. In West Pakistan Minton (1966:86) noted eggs from early April through July and hatchlings from late May to early August. He recorded incubation of 57 days.

Hemidactylus frenatus.—This was one of three house geckos studied by Church (1962) in Java. He found that mating, egg-laying, and hatching occur throughout the year with little indication of seasonal trends. However, farther north in the Loo Choo Islands, Fukada (1965:75) stated that the hatching

season is July to August. Loveridge (1947:129) reported numerous eggs and young in Kenya, May 10 to 14. On Tinian Island of the Mariana Group in the western Pacific, Cagle (1946a) observed geckos probably of this species (though reported as *H. garnotii*) during the period March to July 1945. Throughout this time there were eggs in all stages of development.

Hemidactylus garnotii.—McGregor (1904:115) reported seven incubated eggs on Maui, Hawaiian Islands, on December 27. One hatched on January 13. Kluge and Eckardt (1969) have demonstrated that this is a triploid, parthenogenetic, all-female species.

Hemidactylus longicephalus.—In Angola, Manças (1963:227) reported two females each containing two eggs in August.

Hemidactylus mabouia.—Loveridge (1947:173) reported the finding of eggs in East Africa on the following dates: February 26; March 3 and 4; May 13, 15 and 25; July 29; August 2; October 4 and 16; November 17; and December 4 and 20. Loveridge also cited FitzSimon's record of finding numerous eggs in southern Rhodesia in December. Probably near the equator breeding occurs throughout the year.

Hemidactylus mercatorius.—In Nyasaland, Loveridge (1953:166) reported hatching of eggs of a coconut-palm gecko on January 28, February 14, and February 28. Two gravid females were found on January 12, and eggs were found on February 16.

Hemidactylus persicus.—Minton (1966:84) observed that in West Pakistan eggs have been found from late July to mid-September.

Hemidactylus triedrus.—Minton (1966:85) observed that in West Pakistan females contain large eggs in May and June and the small young are plentiful in September and early October.

Hemidactylus turcicus.—Minton (1966:84) observed that at Karachi, West Pakistan, hatchlings and females containing large eggs have been seen during every month.

Heteronotia

These are small terrestrial geckos. In northern New South Wales, Australia, Bustard (1968c) found a short annual breeding season in *H. binoei* with gravid females present only between October and December. Hatching occurs from the end of February to late March, after 47 or 48 days incubation. Most females breed in their second summer when about 19 months old, but in some breeding is delayed until a year later.

Lepidodactylus

These small geckos are widely distributed over Polynesia and the East Indies and occur also in Malaya and Ceylon. Oliver and Shaw (1953:85) wrote of *L. lugubris*, "In the Hawaiian Islands this gecko breeds throughout the year and there seems to be no definite peak in mating activity." They mentioned one mourning gecko found at Pearl Harbor on October 1 just after

it had deposited an egg. On October 10 it was found to have another egg ready for laying. The same authors mentioned that a captive female laid an egg on January 31, 1945, and on May 3, 92 days later, the egg was found to have an almost fully developed embryo, which perhaps had been somewhat delayed in its development by the relatively cool surroundings in the closet where the egg was kept. Loveridge (1948:334) mentioned two adult females collected at Gusiko, New Guinea, on April 5; one contained large eggs but the other was spent.

On Tinian in the Mariana Islands, Cagle (1946a:9) collected eggs of this species from March to July and found them to be in all stages of development, indicating a long breeding season.

In September and October, 1966, John H. Fitch visited Baker, Hull, Enderbury, Howland and Swains Islands in the central Pacific; he found gravid females on Howland and Enderbury in September, and in October he found gravid females and eggs on both Howland and Baker.

Lygodactylus

This genus includes the dwarf geckos, a group confined to tropical and southern Africa.

Lygodactylus angularis.—Loveridge (1947:222) stated that 15 females collected in Tanganyika, February 14 to 19, contained eggs in various stages of development. In Nyasaland, Loveridge (1953:168) mentioned an interrupted mating on August 26 and eggs observed on September 4, 23, and 30, and December 12.

Lygodactylus capensis.—Loveridge (1947:211) recorded gravid females from Mozambique collected February 8 and 9, and May 27. He mentioned clutches of eggs (always in pairs) found in southern Rhodesia, December 10, and eggs found in Nyasaland on January 8, February 18 and March 17

Lygodactylus conradti.—Loveridge (1947:205) recorded one egg found in Tanganyika on November 20, and a cluster of 102 other freshly laid eggs found on December 21.

Lygodactylus grotei.—Loveridge (1947:215) mentioned eggs found on March 23 and 25, July 10 and 27 (the latter hatched on October 16), October 22, and November 9, 11 and 15. Obviously breeding occurs through much of the year.

Lygodactylus picturatus.—Loveridge (1947:226-235) recorded eggs in Kenya and Tanganyika on January 1, February 1, April 11, June 10, July 5, October 29 and 30, and December 4. Reproduction probably occurs throughout the year.

Pachydactylus

This is a South African genus of geckos with many species, some of which range northward into the tropics.

Pachydactylus bicolor.—Loveridge (1947:361) stated that in Southwest Africa the eggs could be found in June or July.

Pachydactylus capensis.—FitzSimons (1943:103) stated that in South Africa the eggs are laid in summer, but Loveridge (1947:383) recorded two hatchlings caught in Transvaal on November 2, both having eggshells still adhering to them.

Pachydactylus geitje.—On October 27, 1955, Bustard (1963a:434) received in Scotland 50 adults of this gecko from Robben Island off Capetown, South Africa. Several clutches of eggs were laid in November, two eggs per clutch in each instance. Two of the eggs hatched after 122 days of incubation.

Pachydactylus punctatus.—FitzSimons (1943:72) stated that in South Africa the eggs are laid in pairs under stones in midsummer. In Southwest Africa, Loveridge recorded eggs from the opposite time of year (May to July) and he recorded eggs in East Africa and in southern Rhodesia in January.

Pachydactylus scutatus.—Loveridge (1947:360) recorded eggs from Damaraland, June 16 to 19.

Pachydactylus weberi.—Loveridge (1947:394) recorded a large communal nest site with many eggs and empty eggshells, in Great Namaqualand, July 31.

Peropus

This is a genus of stubby-bodied, short-toed geckos, widely distributed in Southern Asia and neighboring islands, Australia and Polynesia. Fukada (1965:76) stated that hatching of *P. mutilatus* occurs in July and August in Japan, but Church (1962:262) found year-round breeding in Java. Loveridge (1948:332) recorded hatching at Finschaven, New Guinea, in early August. There are two eggs per clutch.

Phelsuma

The small geckos of this genus are confined to islands of the Indian Ocean —Madagascar, and the Comoros, Seychelles, Mascarenes and Andamans. Loveridge (1947:299) recorded a gravid female of *P. madagascarensis* on Pemba Island, December 3.

Phyllodactylus

These small, delicate geckos occur in the tropics and subtropics of the northern and southern hemispheres. The four species for which data are available seem to indicate year-round breeding where the climate is sufficiently warm, and a spring and early summer breeding season farther from the equator.

Phyllodactylus lineatus.—In South Africa FitzSimons (1943:27) stated that eggs were laid in early spring; Loveridge (1947:248-250) recorded eggs from Cape Province on August 23 and August 18 to 24.

Phyllodactylus magnus.—Davis and Dixon (1961:39) wrote that in the Chilpancingo region of Guerrero, western México, females had enlarged ovarian follicles and enlarged oviducts in late June and early July. A juvenile of 37 mm snout-vent length was recorded on June 26. In Chiapas, México, Alvarez

del Toro (1960:71) found that clutches of two or more [sic] eggs are deposited from December to April.

Phyllodactylus tuberculosus.—In Sinaloa, Mexico, Hoddenbach and Lannom (1967:295) observed seven gravid females of which five each had two eggs (in left and right oviducts) and two each had one egg—in the right oviduct. Four of the seven females had ovarian follicles 4 to 7 mm in diameter, indicating that there is more than one laying per season, and possibly reproduction throughout the year. The authors noted a low ratio of weight of clutch to body weight (5.5 to 7.2 per cent) in this gecko as compared with certain terrestrial lizards, and they suggested a correlation with the scansorial habits of the gecko.

Farther south, in the Isthmus of Tehuantepec, Dixon (1964:104, 105) found mature eggs throughout the year in females of *P. tuberculosus* and *P. muralis.*

Phyllodactylus xanti.—In southern California Dixon (1964:104) found that hibernation in this species lasts from late October to mid-March. Young of the year begin to appear in mid-June and are found through August.

Ptychozoon

These arboreal geckos of southeastern Asia and neighboring islands have webbed feet, and have wide flaps of skin on the sides of the body and tail that serve for concealment and seemingly for limited downward gliding from branch to branch or from tree to tree. Loveridge stated of *P. kuhlii* "In Java the incubation period is said to last five months (November to May)." Possibly this statement was based upon the same record cited by Smith (1935: 120) of a female of *P. lionotum* in Java which laid two eggs in November; hatching occurred the following May.

Rhotropella

This is a monotypic endemic South African genus of clawless, diurnal, saxicolous geckos. FitzSimons (1943:123) found that in August females of *Rhotropella ocellata* each contained two eggs ready to be laid.

Rhotropus

This is a genus of South African diurnal desert geckos. Loveridge (1947: 290) stated that in Southwest Africa the eggs of *Rhotropus barnardi* are laid in May and June. FitzSimons (1943:121) found that in June females of *Rhotropus boultoni* each contained two eggs.

Teratolepis

This is an endemic monotypic genus of West Pakistan. Minton (1966:88) observed that in southern West Pakistan the same female of *Teratolepis fasciata* may lay several clutches of two eggs each in one season and that the first clutch may be laid in early March.

Thecadactylus

This genus includes large, arboreal, Neotropical geckos. Beebe (1944:158) reported that a female of the turniptail, *T. rapicaudus,* in British Guiana laid an egg in a vivarium on August 25, 1922.

Tropiocolotes

These are small geckos of North Africa and southwestern Asia. Minton (1966:81) found hatchlings of *Tropiocolotes helenae* in West Pakistan in February, July and September—evidence that there is breeding activity throughout much of the year.

Sphaerodactylinae

This subfamily contains five genera of small Neotropical geckos that, unlike most other geckos, are voiceless. According to Taylor (1956:19) a single egg is produced and the records here accumulated, except for Beebe's (1944:148) of *Sphaerodactylus molei,* seem to bear out this statement. However, the reproductive potential may be fairly high because a new ovulation often follows oviposition, and presumably an individual female could produce many eggs in the course of a year.

Gonatodes

These small arboreal geckos evidently produce one egg at a time over a long breeding season, but with one or more seasonal peaks of breeding activity in the course of a year.

Gonatodes albogularis.—Beebe (1944:148) reported hatching of an egg on March 1, 1942, at Kartabo, British Guiana. At Barro Colorado Island in the Canal Zone, Swanson (1945:212) found six eggs of *G. a. fuscus* beginning to hatch on November 29, 1943. He stated that many young had appeared in the vicinity in the preceding days, implying that there is a limited breeding season and that hatching is limited to certain times of year. However, Breder (1946:426) found both eggs and young at Colón, Panamá, in late January.

Evidence of an extended breeding season is provided by 75 Costa Rican specimens in the University of Kansas Museum of Natural History; 25 were collected by me in the second week of March, 1965. Six of the eight adult females in this group were gravid, and there were young of the following sizes (snout-vent lengths in millimeters): 23, 24, 24, 27, 29, 30, 36, 36, 36. Breeding through the winter months is indicated. Fifty specimens were collected in July and August, mostly on the 27th and 3rd, respectively. All of 18 adult females of this group had either an oviducal egg or a more or less enlarged ovarian follicle. The series included young of the following sizes: 18, 19, 20, 22, 23, 26, 32, 32 and 33 mm. The combined records seem to indicate breeding throughout the year or most of it in Costa Rica. Each gravid female examined by me contained a single egg.

Gonatodes annularis.—At Kartabo, British Guiana, Beebe (1944:150) recorded the following field notes: April 29, 1922—an egg found washed up on riverbank; July 18, 1920—five eggs found; July 23, 1922—4 eggs found. They were kept and hatched on August 17 and September 13; August 23, 1919—an egg found hatching in a palm stub. These few records indicate a long breeding season; perhaps egg-laying occurs throughout the year.

Gonatodes concinnatus.—A series of 75 in the University of Kansas Museum of Natural History from Limón Cocha, Napo, Ecuador, June 1966, were examined. Twenty-two adult females, most of those of adult size, were carrying a single egg apiece. The smallest gravid female was 32 mm in snout-vent length and most adults were 35, 36 or 37 mm. There were also young of various sizes; three were 16 to 20 mm, five were 21 to 25, and nine were 26 to 30. It seemed that reproduction had been continuous for several months and perhaps it occurs year-round in this equatorial region.

Gonatodes taniae.—Test, Sexton and Heatwole (1966:10) collected these lizards at Rancho Grande, Venezuela, through most of the year and concluded that the greatest numbers of hatchlings might be recruited to the population in the rainy season, but that hatching might occur at any time of year. Newly hatched young 22 to 24.4 mm in snout-vent length, with evident umbilicus, and characteristic pattern and behavior, were captured on the following dates: March 11; May 1; June 3 and 29; July 13, 23, and 24; September 23; and October 3. This small sample indicates hatching from late February to October. Allowing an estimated two months for incubation, and including an additional record of a female carrying a large unlaid egg on November 29, there is evidence for egg-laying in every month except October and November.

Gonatodes vittatus.—Quesnel (1957) studied a population of the streak gecko in Trinidad. Eggs were present every month of the year, as seasonal change is slight. Females were found to lay at approximately monthly intervals. They were found to produce fertile eggs for as much as five or six months after mating.

Sphaerodactylus

These are small Neotropical geckos that occur as far north as the southern tip of Florida.

Sphaerodactylus cinereus.—Carr (1940:71) wrote that on Key West, southern Florida, eggs of the ashy gecko are laid in August.

Sphaerodactylus glaucus.—In British Honduras, Neill and Allen (1959:33) collected an egg on July 14, 1959; a hatchling emerged on August 18, 1959. On May 13, 1939, at Alvaro Obregón, Tabasco, Smith (1949:34) found many eggs ready to hatch, as well as adults, under the loose bark of trees.

Sphaerodactylus molei.—At Kartabo, British Guiana, Beebe (1944:155) obtained a female containing two eggs almost ready to be laid, on March 16, 1924, and on July 30, 1919, he found two eggs in a rotten stump.

Sphaerodactylus notatus.—In southern Florida, Carr (1940:71) reported that eggs of the reef gecko are laid from June to August. However, Duellman

and Schwartz (1958:276) found seven eggs on December 29, 1951. Five of these hatched 74 days after they were found and the remaining two hatched after 79 days. On Key West on March 8, 1952 they found a communal nest in a termite-ridden log which contained 280 eggs.

Iguanidae

The iguanids comprise one of the most diverse families of lizards, with a large number of species, ranging from small to large. Most are terrestrial, but many are scansorial. Essentially this is a New World family, occurring from southern Canada southward throughout the American tropics including the West Indies, and into temperate South America, with greatest abundance and diversity in the southwestern United States and on the Mexican Plateau. Also there are relict Old World genera in Madagascar and Fiji. Most iguanids are oviparous but viviparity has been attained independently in several different genera, seemingly always in response to relatively cool climates. *Phymaturus*, at least, is exclusively viviparous. In both temperate and tropical climates many iguanids have well-defined breeding seasons, often with only a single clutch laid per year. In the tropics the seasonal distribution of rainfall seems to be the chief determining factor. In both temperate and tropical areas some kinds seem to lack well-defined breeding seasons but may breed year-round, or throughout much of their season of activity. Several fairly well-defined subfamilies have been recognized, such as Anolinae, Iguaninae and Sceloporinae. However, these groups are so large and ecologically diverse that they are not especially useful in the present context. The anoles differ from most of the other iguanids in their reproductive habits. They are slender, active, often arboreal and mainly tropical lizards; unlike other iguanids, they normally lay only one egg at a time, and eggs may be produced in fairly rapid succession—the left and right ovaries and oviducts alternating in a regular and sometimes continuous cycle.

Amblyrhynchus

This monotypic genus is endemic to the Galapagos Islands. Although these large iguanas occur only in the vicinity of the equator, in an equable year-round climate, accounts of their habits indicate that there is a relatively short and concentrated breeding season. Egg-laying occurs toward the end of the rainy season.

Amblyrhynchus cristatus.—Carpenter (1966) recently published a detailed account of the marine iguana's ecology, supplementing less complete accounts

of many earlier observers. According to Carpenter, the breeding cycle is timed to avoid the *garúa* season, a period when damp, heavy mist hangs over the islands, approximately from June into October. The breeding season starts in December on Narborough Island, and about one month later on Hood Island. Egg-laying, and the breakdown of territoriality in the males occurs in late January and early February on Narborough. Bartholomew (1966:245) observed marine iguanas under natural conditions in January and February, 1963. The breeding season had terminated at some time prior to his arrival, but within the period of his stay, egg-laying began and reached its peak, with dozens of females gathered on the beach in a small area digging nest holes and fighting among themselves. He mentioned egg-laying on February 3 and 4 and stated that the clutch consisted of two large eggs. From a study of natural nests he determined that incubation normally occurs within the temperature range 28° to 30° C.

Eibl-Eibesfeldt (1961:70) stated that ". . . the female digs a hole approximately one foot deep in the sandy areas of the beach in which she deposits the only two eggs that she lays during the period of one season. After the eggs have been laid, the hole is carefully covered. As these sandy areas are often scarce, females often compete for them and fight in the same manner as males." He described in detail the jousting of males, but explained that it was limited to the breeding season and at other times the males were more tolerant of each other.

Carpenter (1966:363) excavated 16 nests and found 29 eggs in them. One nest contained six eggs (believed to be two clutches of three eggs each), three other nests had three eggs each and the remaining 12 nests each had two eggs. Shaw (1966:585) received a female at the San Diego Zoo on February 24, 1964, and it had already laid an egg *en route*. The following day it laid two more eggs; the first egg was rendered inviable by desiccation. The other two eggs were incubated at temperatures ranging from 80° to about 95° F; hatching began after 112 days.

Anolis

The anoles comprise a large genus (with 165 species according to Schmidt and Inger, 1957:120). They are fine-scaled, of small or medium size, with light and slender bodies, large hind legs and very long tails. Although some species are mainly terrestrial, scansorial tendencies are strongly developed in the group as a whole. The anoles are mainly Neotropical, with most of the species in South America, Central America and the West Indies. The single egg, which is the normal complement at each oviposition (for most species, at least), is seemingly dropped rather carelessly instead of being buried in a specially constructed nest burrow.

Anolis barkeri.—Kennedy (1965:42) observed and collected several of these semi-aquatic anoles at Volcán Santa Marta in Veracruz, México. A captured female laid two eggs in her container on July 7, and when dissected she was found to have an enlarged follicle in one ovary.

Anolis biporcatus.—This is a giant species of central America and northern South America. Beebe (1944:199) observed the species in British Guiana, and collected records of courtship activity and oviposition; without differentiating

between them he noted the following numbers for these two types of observation combined: March—2, April—1, May—3, June—7, August—2. In central Petén, Guatemala, Stuart (1935:42) found that females contained one or two fully developed eggs in April and May.

Anolis carolinensis.—This common anole of the southeastern United States is by far the northernmost representative of the genus. Its habits, ecology and natural history have been studied by several workers. Fox and Dessauer (1958b:196) found that males attain sexual maturity in the first year, after six to eight months of rapid growth. They found that those below 55 mm snout-vent (a length attained by some within two months of hatching) might produce motile sperm but still had the accessory sex organs not fully developed. Fox and Dessauer (1958a:438) found that in male anoles spermatogenesis is initiated in autumn and is influenced by decreasing day length, and continues through the winter, spring and early summer. In August the sex organs regress. At that time the appetite is high and storage of fat and glycogen is tremendously increased. Carr (1940:71) wrote that in Florida mating occurs in April and May, and eggs are laid in June and July. However, Hamlett (1952:183), studying the species in the field and laboratory at New Orleans, found that the breeding season extends from mid-spring until the end of summer, and that the two ovaries alternate in producing eggs, which are laid singly at intervals of about two weeks. Each egg ovulated requires 18 to 19 days to complete its development, mature, and pass down the oviduct.

Anolis chrysolepis.—Series of *A. c. scyphens* in the University of Kansas Museum of Natural History were obtained in rain forest at Santa Cecilia, Napo, Ecuador in June 1966 and March 1967. Among nine collected in June there were three gravid females, but among 18 collected in March there was only one gravid female and most were immature.

Anolis cobanensis.—In Guatemala, Stuart (1942:7) recorded a female that "contained several fully formed eggs" on May 24.

Anolis crassulus.—In Guatemala, Stuart (1942:4) found that females contained large eggs in the middle and latter parts of May at altitudes of 1700 and 1800 meters.

Anolis cupreus.—I observed this species at Playas del Coco, Guanacaste Province, Costa Rica, in late March—the dry season. Two adult females collected then did not have enlarged ova. In the University of Kansas Museum of Natural History two of three females collected in June, all four of those collected in July, and five of the six collected in August were gravid. The species occurs in an area characterized by seasonal droughts and seemingly its breeding is limited to the wetter parts of the year.

Anolis dunni.—In the Chilpancingo region of Guerrero, México, Davis and Dixon (1961:40) noted developing ova (4 mm in diameter) in females in early June, and large eggs ready for deposition in late June and early July.

Anolis fuscoauratus.—Beebe (1944:200) observed "breeding males" in British Guiana and Venezuela on May 10 and 16, on August 9, and on December 31. On May 12 he examined a female which had one egg fully developed and ready to be laid, and another partly developed. I examined 204 collected

at Santa Cecilia and Limon-Cocha, Napo, Ecuador, in June 1966 and March 1967. Nearly all adult females were gravid and there were young of various sizes in both these months.

Anolis gadovi.—In the Chilpancingo region of Guerrero, México, Davis and Dixon (1961:40) obtained a female containing two shelled eggs on July 2.

Anolis humilis.—This small ground-living anole is one of the most abundant Central American species. I observed it in February and March, 1965, and examined 214 in the University of Kansas Museum of Natural History. Most of the adult females (31 to 49 mm snout-vent) were gravid, as follows: nine of 10 collected in March, all six collected in April and May, 50 of 52 in June, 20 of 21 in July, all eight in August, and all four in November. Although the winter months were not represented in the sample, young from near hatchling size up were well represented in the series collected by the writer on March 6 at Puerto Viejo, Heredia Province, Costa Rica, indicating that year-round breeding had occurred. The evidence suggests that most mature females produce eggs continuously.

Anolis lemurinus.—This is a medium-sized Central American species. Stuart (1948:49) noted that in Alta Verapaz, Guatemala, females contained well-developed eggs in mid-May. Thirty-six from Guatemala were examined by me. The only adult female collected in February lacked enlarged ova, as did three collected in March, but all six adult females in a June sample were gravid. The meager data available suggest the possibility of seasonal restriction of breeding.

Anolis leptoscelis.—I examined a series of 19 in the University of Kansas Museum of Natural History collected at Santa Cecilia, Napo, Ecuador, in March 1967. There were five gravid females, each containing two eggs of different sizes. Also there were young of graded sizes.

Anolis limifrons.—Sexton, Heatwole and Meseth (1963:490) studied a population of this abundant small anole in central Panamá. In a March and April sampling they found no eggs in the field, no young, and females contained no oviducal eggs and only a few enlarged ovarian eggs. In June and July in the same area eggs were found in abundance, and there were many gravid females. At this time of year the population consisted of young 16 to 26 mm snout-vent and adults, 38 to 42 mm. In a December-January sample, all but one were in the 28 to 48 mm range, large young and adults. It seemed that reproduction virtually ceased in winter, and in the March-April dry season. Field work by the same authors has continued in a trans-Isthmus transect. Sexton (personal communication, January 1967) stated that it is ". . . clear that reproduction goes on at full tilt during the wet season and is slowed down completely or partly during the dry season, depending on conditions." He cited an instance when a sudden heavy rain in the dry season caused a notable shift in the reproductive status of females, and within a few days many had developed enlarged ovarian follicles or oviducal eggs.

I observed these anoles in the field in March 1965, and examined 299 specimens in the Museum of Natural History, all from the Atlantic slope of Costa Rica, where annual precipitation is high and the spring dry season is much less marked than in some other parts of Central America, including the

site of the study by Sexton *et al.* in Panama. Most of the mature females (33 mm or more snout-vent) were gravid, as follows: all ten collected in March; 36 of 37 collected in June; 40 of 41 collected in July; 23 of 26 collected in August, and three of four collected in September. Each series contained a substantial number of young, and it is notable that in each instance the young were of graded sizes, from those recently hatched to those approaching minimum adult size. Although nearly half the year is unrepresented by the data at hand, the available evidence suggests year-round breeding in the Costa Rican rain forest. Each gravid female contained two eggs in different stages of development.

Anolis lionotus.—This is a medium large species characteristic of streamside habitat in humid tropical or subtropical forest. I examined 58 from Costa Rica, collected in March, June, July, and August. Most of the adult females were gravid, as follows: 10 of 12 collected in March; one in June; and all six collected in July. The only female collected in August was not gravid. Young were well represented in the March, July, and August series. With the limited data at hand it can only be said that breeding extends through late winter, spring and early summer, but perhaps it continues throughout the year.

Anolis megapholidotus.—Near Chilpancingo, Guerrero, México, Davis and Dixon (1961:40) found that females were gravid in June.

Anolis nannodes.—In Alta Verapaz, Guatemala, Stuart (1948:50) found females with well-developed eggs in May.

Anolis nebulosus.—In the vicinity of Chilpancingo, Guerrero, México, Davis and Dixon (1961:41) found numerous females gravid in June and July. They stated that these gravid females contained one to three (usually two) enlarged ova.

Anolis nitens.—Beebe (1944:200), observing this species in British Guiana and at Caripito, Venezuela, recorded breeding in April (13 records), May (nine records), June (five records), July (two records), and August (two records). In this region there is a rainy season in May, June, and July and a shorter one in December and January, with dry seasons intervening.

Anolis omiltemanus.—Davis and Dixon (1961:41) found two gravid females on June 11, and two more on June 24, at Chilpancingo. Each female contained two ova.

Anolis pentaprion.—At Palenque, Chiapas, México, Smith and Kerster (1955:201) obtained 49 hatchlings in the period July 7 to August 2 from eggs collected in bromeliads but no adults were seen.

Anolis sagrei.—In southern Florida Duellman and Schwartz (1958:283) noted mating on July 13 and August 13. Hatchlings were found in Miami on June 12 and 25, 1953. An egg laid in a terrarium on July 14 hatched on August 29.

Anolis tropidolepis.—This is a montane species. I examined a series of 93 from central Costa Rica collected from March through August. Nearly all the females of adult size (42 to 52 mm snout-vent) were gravid, as follows: all three collected in March, the only one from April, all five from June, 24 of 26

from July, and seven of 10 from August. The months September through February are not represented, but it can be assumed that breeding extends through most of the year or all of it, since the known breeding season extends from the dry season throughout most of the rainy season, and otherwise seasonal variation within the range is slight.

Basiliscus

The basilisks are medium-sized oviparous terrestrial iguanids of tropical Central America. There may be year-round breeding in *B. vittatus* in tropical rain forest habitat of the humid east Coast, but seemingly breeding activity is more concentrated at certain times of year. *B. basiliscus* occurs where there is a long dry season, and the breeding season seems to be short and well defined.

Basiliscus basiliscus.—On March 18, 1965, I obtained 21 of these lizards and saw many others at Rio Higueron, Guanacaste Province, Costa Rica. One hatchling was captured and several others of similar size were seen but escaped. The remainder of the sample consisted of adults over a wide size range, and large young. Seven females considered to be adults (more than 115 mm snout-vent) had enlarged oviducts, but their ova were minute and none was gravid. It seemed that the females had oviposited some weeks earlier, probably in January. That the breeding season had been brief and concentrated was indicated by the fact that there were neither gravid females, nor young between hatchling and adolescent size. In the seasonally dry climate of Guanacaste, the breeding season may be more restricted than it is in areas of more equably distributed rainfall. On Barro Colorado Island, Panama Canal Zone, Netting (1936:116) reported newly hatched clutches on March 7 and 8, 1934. Ortleb (1965:277) in the same area found a female laying on June 24, 1963; 18 eggs were found and these hatched on October 8, 1964, after 77 days of incubation.

Basiliscus vittatus.—The banded basilisk is widely distributed in lowland tropical areas of Central America. I examined 92 in the University of Kansas Museum of Natural History, all from late winter, spring and summer. Those from January, February, March, and April were adults and young that were more than halfgrown. Young not much larger than hatchling size were present in the July and August series. Gravid females were represented as follows: one of three in February, two of three in March, all of three in April, one in June, four of nine in July, three of seven in August, and none of one in September. Hirth (1963a:101), who studied these lizards in a coastal area of northeastern Costa Rica, concluded that there is some breeding all year round, but that it is concentrated in late spring and early summer, for young are much more abundant in August and September than at other times. In Chiapas, México, Alvarez del Toro (1960:80) reported egg-laying to occur in April, May, or June, with young hatching in the rainy season. Near Chilpancingo, Guerrero, México, Davis and Dixon (1961:41) suggested that the breeding season lasted from April to July. In the latter half of June adult females (more than 70 mm snout-vent) were gravid. In central El Petén, Guatemala, Stuart (1935:44) recorded a hatchling found on June 17 at the beginning of the wet season. In British Honduras, Neill and Allen (1959:37) observed hatchlings to be abundant in July but saw none in April. Smith and

Laufe (1945:331) mentioned a female containing seven oviducal eggs at Boca del Río, Veracruz, México, July 20-21, 1942. Smith (1935:142) mentioned a female containing three eggs in a collection from Guerrero and Veracruz, June 28 to July 16.

In 13 gravid females dissected by the writer the clutch averaged 4.07 ± .30. In all but two the clutch numbered 3, 4, or 5 eggs, and the mean approximated that of 4.2 found by Hirth (1963a:101) in 25 females at Tortuguero. However, Alvarez del Toro (1960:80) stated that the usual clutch in Chiapas is a dozen eggs, and Conant and Downs (1940:34) reported a clutch of 14 eggs laid in captivity.

Callisaurus

These are cursorial desert lizards of the southwestern United States and México. In the northern part of the range where the growing season is relatively short, there is a brief breeding season, but farther south the breeding season is more protracted and probably females produce several successive clutches.

Callisaurus draconoides.—The zebra-tailed lizard occurs in desert regions from northwestern Nevada south far into México. Stebbins (1954:221) stated that seven gravid females averaged four eggs apiece (two to six) and that females were found with large eggs in late June, July, and late August. In the series that I examined two females each contained five eggs and three contained four eggs; these combined with Stebbins' records indicate an average of 4.16 eggs.

I examined 33 from Washoe County, Nevada; none of five adult females collected in May was gravid, but four of five collected in late June and one of four collected on July 21 were gravid. The gravid female from July had a snout-vent length of 62 mm whereas the non-gravid females on the same date had snout-vent lengths of 79, 77, and 76 mm. It is surmised that first-year young reach maturity, but produce eggs a little later than old adults. In northern Nevada the growing season is relatively short and females may produce only one clutch per season. In the southern part of the range the growing season is much longer, and multiple clutches may be the rule. A female of only 54 mm snout-vent, from Baja California, March 14, was gravid whereas six larger ones also collected in early spring in the same region were non-gravid. The gravid female must have been considerably less than a year old. In San Bernardino County, southern California, the ratio of gravid to non-gravid females for several months was as follows: April—1 to 5; May—2 to 2; June—4 to 6; July—1 to 6. In the early spring series of 61 from Baja California the greatest concentration (19) falls in the size range 59 to 65 mm snout-vent but otherwise there is fairly uniform distribution, from a hatchling only 29 mm in length to the largest adult, 78 mm, again indicating an extended breeding season.

In a population study at Phoenix, Arizona, William S. Parker (MS) found an average of 4.5 eggs (2 to 7) in 19 gravid females. He found females with enlarged ovarian follicles or oviducal eggs from April through August, and found hatchlings from July to November. From analogy with the somewhat similar *Holbrookia texana,* having a breeding season of about the same length

in Texas, Parker surmised that a female might produce as many as five clutches. He found that females mature and produce eggs in their first year; those hatched in fall lay for the first time the following July or August.

Corytophanes

These are medium-sized, crested, arboreal iguanids of Neotropical forests. There are both oviparous and viviparous species.

Corytophanes cristatus.—Duellman (1963:235) noted that a female captured in southern El Petén, Guatemala, on June 28 contained eggs 11 mm in diameter. In the same area Stuart (1958:22) reported a juvenile in early April. Ream (1965:239) recorded that a female captured at Barro Colorado Island, Canal Zone, on August 21, 1961, and taken back to the University of Wisconsin, laid six eggs on February 5, 1962. Although the female had no contact with a male in the 5½-month interval, the eggs were fertile, and one hatched on July 2, 1962. The other eggs failed to hatch but contained fully developed embryos. Gravid females in the University of Kansas collection were taken on the following dates: June 28 (8 eggs, 12 mm in diameter); July 16; October 1 (5 uterine eggs, 28 mm in length). Nongravid adult females in the collection were taken on the following dates: March 3, July 17, August 8, August 13, September 9 (two collected on August 13 and the one collected on September 9 had enlarged oviducts and may have oviposited shortly before collection); August 8. These few available records indicate that breeding and egg-laying occur throughout much of the year.

Taylor (1956:166) found a female ovipositing, at Golfito, Costa Rica, on September 9, 1952. The eggs were being deposited in a cavity that the female had dug in the hard soil of a forest path; there were six in the clutch.

Corytophanes hernandesii.—Alvarez del Toro (1960:86) wrote that in Chiapas, México, the female of this species lays three or four eggs from May to July. In El Petén, Guatemala, Stuart (1935:44) obtained a hatchling on May 24, and (1958:22) a juvenile in mid-March.

Corytophanes percarinatus.—McCoy (1968a:176) determined that this montane Guatemalan species is viviparous. Ovarian follicles begin to enlarge in late June, and in December females contain large eggs. Births are thought to occur in late spring; four females in late May and June had quiescent ovaries and enlarged oviducts indicating recent births. In 36 females there was an average of 7.1 eggs or embryos. The finding of nonreproductive females of 83 and 86 mm snout-vent in early August and early October was interpreted by McCoy as evidence that females do not breed until the second summer after birth.

Crotaphytus

This genus consists of five species characteristic of arid regions of the western United States and adjacent México. All conform to the same general seasonal pattern of behavior, with breeding in late spring and early summer, and hatching of young in late summer. Even at the northern edge of the range adult females have the potentiality of producing two clutches in a season. It is

not known whether under favorable conditions more than two clutches per year are produced.

Crotaphytus collaris.—Reproduction in the collared lizard is best known from my (Fitch, 1956) study in northeastern Kansas on the edge of the natural range. In this area breeding occurs in May and June; eggs are deposited in June or early July. Young may attain sexual maturity by the following spring. For 13 first-year females (77 to 87 mm snout-vent) the clutch averaged 3.7 eggs, for 11 presumed second-year females (90 to 97 mm snout-vent) the clutch averaged 6.1, and for nine old adults (98 to 108 mm snout-vent) the clutch averaged 8.3. Some first-year females do not produce eggs, and more rarely second-year females are unproductive, whereas old adults sometimes produce two clutches in a season. One female of a small colony on the University of Kansas Natural History Reservation produced two clutches in both 1952 and 1953. In both years the first clutch of this female was laid in the second week of June and the second clutch in the first week of July. Several other large females in the same colony produced only a single clutch each year. Farther south in the species' range, where the growing season is longer, the opportunity for producing multiple clutches seems to be greater because of the longer growing season.

Robison and Tanner (1962:26) listed 47 clutches of *C. collaris*, which averaged 6.7 eggs (2 to 21). This average was raised by records of two unusually large clutches of 16 and 21 reported in the literature, but considered highly questionable in both instances by Robison and Tanner, because: "Uncontrolled conditions existed in both cases, since Ditmars . . . apparently had several lizards within the same enclosure, and the observation of Burt and Hoyle (1934:198) was made in the field."

Among the clutches listed by Robison and Tanner were 20 of the western collared lizard, mostly from Utah, but including a few from northern Arizona, Nevada, southern California, and Idaho, and this group averaged only 4.65 (3 to 8) eggs, whereas 33 clutches of the eastern collared lizard, recorded by me from eastern Kansas, averaged 5.76 (1 to 12) eggs.

Crotaphytus reticulatus.—Werler (1951:37) recorded that a female collected in Starr County, Texas, on June 1, 1950, died on July 24 containing eggs almost ready to be laid.

Crotaphytus wislizenii.—The leopard lizard is one of the most carnivorous iguanids, living to a large extent on smaller lizards. It is notable in that the female is larger and more robust than the male. As in many other iguanids, the inseminated female develops reddish markings; in the leopard lizard these markings are especially bright and concentrated.

In Mesa County, west-central Colorado, McCoy (1967:147) found that in both sexes maturity is attained late in the second year, and that females lay a single clutch (average 7.3 eggs in ten clutches) per season. Egg-laying is completed in early July. Robison and Tanner (1962:26) listed 21 clutches, including seven from the literature and others gathered by themselves, in Utah, Idaho and Nevada, which averaged 5.15 eggs (1 to 9). Montanucci (1967:119) mentioned additional clutches of seven and four eggs from females

from southern California. There were complements of 5, 5 and 6 eggs in specimens examined by me.

In a series of 90 leopard lizards from Baja California examined in the course of the present study, seasonal distribution of gravid females was as follows: March, two (the only two females representing this month); April, five (of eight); May, six (of nine); June, three (of six); July, none (there were two nongravid). Obviously in the southern part of the range the breeding season extends over many weeks, and females perhaps produce two or more clutches in a season.

Turner *et al.* (1969) studied a population of leopard lizards in Rock Valley, southern Nevada. They reported an average of 6.2 eggs in nine females in 1968. They found that four of 26 mature females in 1965 and one of seven in 1966 laid two clutches of eggs in a season. During the spring of 1966, due to a combination of favorable circumstances, growth was more rapid than usual, and three of 21 yearling females attained adult size early in the season (at about nine months of age), appeared gravid, and presumably produced eggs. In the less favorable years there was little growth; reproduction was almost negligible in 1963 and did not occur at all in 1964. In occasional maturing and egg-laying of first-year females, and in vacillation of mature females from production of one clutch per season to two clutches or no production, this population paralleled the population of *C. collaris* studied by me in northeastern Kansas. But seemingly much different environmental factors were involved. Turner *et al.* attributed a successful season of reproduction in *C. wislizenii* to heavy rains in late March and early April, with resultant luxuriant growth and fruiting of perennial plants and abundance of associated arthropods, and poor reproduction or total failure to seasons of drought. But in northeastern Kansas, with abundant vegetation and insect prey, reproduction was most successful in relatively dry summers and was inhibited in the 1951 season of heavy rainfall, abnormally low temperature and frequent cloud cover.

Montanucci (1965, 1967) published accounts of the habits of the San Joaquin Valley leopard lizard, *C. silus,* now thought to merit recognition as a distinct species. In this population males and females do not differ in size. Montanucci found that the mating season lasts from late April to early June, and he found evidence of females laying an occasional second clutch in a season. Postnuptial red markings appear in the female approximately a week after mating and reach their peak in two weeks. Average number of eggs in *C. silus* is only three per clutch (2 to 5). Incubation was estimated at 57 days. Hatching was noted to occur from about the first of August into September. In late summer adults are seldom seen, seeming to retire into aestivation, but females are far more active than males at that season, perhaps replenishing their store of fat after having produced eggs.

Ctenoblepharis

This genus includes five species of terrestrial, medium-sized, heavy-bodied, South American iguanids that occur on the western slope of the Andes. They are omnivorous and predominantly vegetarian. Insofar as known they are viviparous. Donoso-Barros (1966:341) reported advanced embryos in female *C. jamesi* in August and also reported viviparity in *C. nigriceps.*

Ctenosaura

The ctenosaurs are large herbivorous iguanids of Mexico and Central America, primarily in arid regions. The available information indicates that wherever these lizards occur they have a short annual breeding season in the drier part of the year.

Ctenosaura acanthura.—In late April, Smith and Burger (1950:167) obtained gravid females in Veracruz which contained 17, 17, and 28 eggs.

Ctenosaura pectinata.—In Morelos, México, Davis and Smith (1953:101) noted numerous small green young, assumed to be recent hatchlings, from late July on, and adults were not in breeding condition in late summer. These authors therefore speculated that breeding must occur early in the year. Similarly, in the Chilpancingo region of Guerrero, México, Davis and Dixon (1961: 43) concluded that breeding must occur in early spring because in the latter half of June adults were sexually quiescent and there were many small greenish young, 59 to 65 mm in snout-vent length, and judged to be not more than a month old. Evans (1951:10) studied behavior in a colony inhabiting a cemetery at Acapancingo, Morelos, México, and he noted that females were laying their eggs in April. One female that was excavating a nest burrow on April 11 had 49 eggs in her oviducts, and another captured on the same date had just completed laying. At La Playa and Coalcoman in Michoacan, Mexico, Duellman (1961:65) observed the bright green, recently hatched young in early July.

Ctenosaura similis.—Alvarez del Toro (1960:93) described the habits of *"Ctenosaura pectinata"* in Chiapas, Mexico, but probably his account is based upon *C. similis,* because Chiapas is outside the known range of *C. pectinata.* The egg-laying season was stated to be March to May, with a clutch of 20 to 30 eggs and a 90-day incubation. Duellman (1965:599) in his study of the fauna of the Yucatan Peninsula, México, noted that juveniles were common on Isla del Carmen in early July, 1962, and on Isla Aguada on June 9, 1963. Burt (1935:170) reported a juvenile 86 mm in snout-vent length from Balboa, Canal Zone, on September 24. In my study 123 were examined, from Yucatan, Nicaragua and Costa Rica. The smallest young examined were a group of 12 hatchlings that averaged 54 mm (49 to 59) snout-vent. These were collected June 3 and 4 near Managua, Nicaragua. Other young not much above hatchling size have been collected in late June, July, and August, as shown in the histogram, Fig. 1.

In late March, 1965, in Puntarenas and Guanacaste provinces, Costa Rica, I observed many of these lizards including adults and partly grown young, but no hatchlings. The smallest young were somewhat less than halfgrown. Two collected that were considered representative of this size group were 140 and 149 mm snout-vent, hence they had nearly tripled in length since hatching, perhaps 9-11 months earlier. Eighty-two individuals that were seen March 20 to 22 were classed as follows in regard to size:

Unusually large adults	11
Medium or small adults and large young	38
Young less than halfgrown	33

In this grouping, "medium or small adults and large young" probably included several age classes, but they did not fall into easily recognizable size

groups. Ten specimens that were collected did not include any unusually large adults, and were of the following sizes in millimeters:

sex	*snout-vent*	*tail*
♀	335	515
♀	277	410 (regenerated)
♀	237	415 (incomplete)
♂	240	340 (regenerated)
♀	201	393
♂	193	75 (incomplete)
♀	173	391
♀	168	350
♀	149	325
♀	140	224

In the two largest females oviducts were enlarged and collapsed indicating that oviposition might have occurred recently, and none of the females seen in the field was obviously gravid. The season of egg-laying was perhaps already completed. The fact that young estimated to be nine months old are still less than halfgrown and that young seemingly belonging to at least one older age group are present with them indicate that sexual maturity is not attained until the third year at the earliest.

Cyclura

This is a West Indian genus of large, heavy-bodied iguanas. Although their range is entirely within the tropics, in an equable climate, the observations cited below suggest that there is a concentrated annual breeding season, perhaps controlled by seasonal precipitation. Limited information concerning the breeding of the Cuban *C. macleayi* was obtained by Shaw (1954:73) from a small colony of the lizards received at the San Diego Zoo in April, 1951. In June, 1952, each of two females, kept in separate pits, mated. Eggs were laid in July by both of them, but both clutches were lost. One of the females laid again in July, 1953, and her eggs hatched after 119 days.

Dipsosaurus

The desert iguanas are medium-sized herbivorous and insectivorous lizards of desert regions of the southwestern United States and northwestern México.

Dipsosaurus dorsalis.—Norris (1953:274) stated that the clutch consists of three to eight eggs and he mentioned a female that died distended with seven large eggs on June 23. Stebbins (1954:213) mentioned females captured near Palm Springs, California, which laid, respectively, six and five eggs on June 27 and August 11 and 13. In his study, Norris found that emergence from hibernation occurs in middle or late March in the Coachella Valley of southeastern California. Testes of the males enlarge rapidly after activity begins, and breeding takes place in April and early May. Gravid females retreat underground for as long as several weeks in late June and early July. At this time there are many adult-sized females which continue to be active above ground and which seem to be nonbreeders, but it was not determined whether they were still immature or were fully adult individuals which, perhaps, breed only

in alternate years. Most young emerge in August, and adults retreat into hibernation in early autumn, at least a month earlier than juveniles. In a study at Phoenix, Arizona, William S. Parker (MS) found evidence of two broods annually, and from the slow growth made by marked individuals he concluded that at the earliest, sexual maturity is attained after three hibernations in the third year of life.

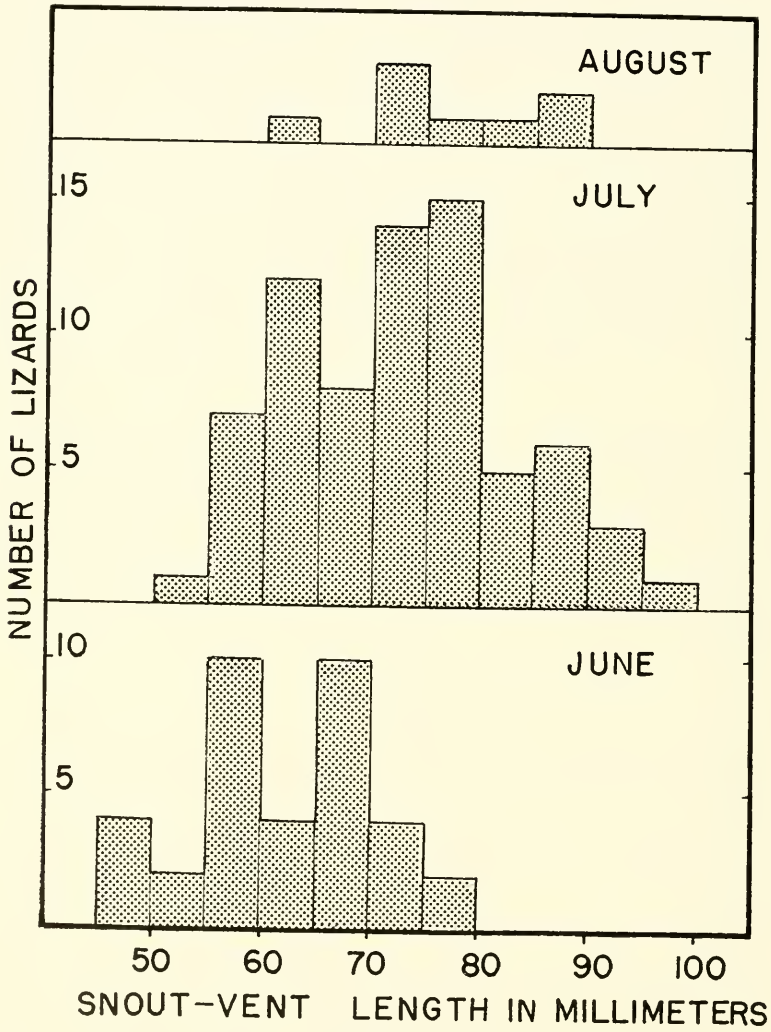


Fig. 1. Snout-vent lengths of hatchling and juvenal ctenosaurs *(Ctenosaura similis)* from Yucatán, Nicaragua, and northwestern Costa Rica. Smallest individuals, near 50 mm snout-vent, were mostly collected in early June, which is presumed to be the time of hatching. Average size had increased markedly by July and August. Large adults are more than 300 mm in snout-vent length.

Enyaliosaurus

These small iguana-like lizards of México and Central America occur chiefly in arid regions, having pronounced seasonal changes—from warm to cool and wet to dry; information available for *E. clarki* indicates a short annual breeding season.

This species is a partially arboreal spiny-tailed lizard of the arid Tepalcatepec Valley in Michoacán, México. Duellman and Duellman (1959:9) observed hatchlings in late June, but there were no gravid females at that time of year, nor in late April. The authors suggested that egg-laying occurred in early April. In late summer the population consisted of three fairly distinct size groups: adults, juveniles not much above hatchling size, and an intermediate group, presumably yearlings.

Holbrookia

There are several species of these oviparous, terrestrial and cursorial lizards, all in xeric habitats of the western United States and México. Females attain sexual maturity late in their first year, and the breeding season is long, lasting from soon after spring emergence until late summer.

Holbrookia lacerata.—This is a species of central and southern Texas. Axtell (1956:177) wrote: "Egg laying apparently takes place twice a year, with the first clutch being deposited in May and June and the second in July and August." He obtained evidence that newly matured females laid from four to six eggs for their first clutches and five to seven for their second, whereas those females that were fully adult laid seven to 12 eggs at a time. Eggs laid on June 25 hatched July 31 to August 2 and another clutch laid on August 23 hatched October 2 to 4.

Holbrookia maculata.—The lesser earless lizard has an extensive geographic range, from North Dakota to southern México. No thorough study of its ecology has yet been made. I observed it in many localities in Kansas and New Mexico and examined series in the University of Kansas Museum of Natural History and the American Museum of Natural History.

A series of 146 from Kansas was examined. In this part of the range specimens are sometimes observed in April but most records are from May, June, July, and August. Those emerging from hibernation in spring are mostly adults, and first-year young that are well above hatchling size, and some are adolescents. Seemingly all these young attain breeding maturity in the season after their first hibernation. Ratios of gravid individuals to others among the adult females examined were as follows: May, 3 to 0; June, 25 to 0; July, 10 to 1; August, 11 to 13. Hatchlings have been collected as early as July 6, and these must have come from eggs laid in early June or late May.

In the southern part of the range the breeding season is longer. A series of 219 were examined from México and southern Arizona and the females showed the following ratios of gravid to nongravid individuals in different months: April, 4 to 26; May, 2 to 1; June, 10 to 6; July, 19 to 6; August, 18 to 3; September, 2 to 1.

For 68 egg-bearing females from both northern and southern parts of the range, the average clutch was 5.58 (10 to 2) eggs. However, averages were

notably different in northern and southern parts as shown by the following figures.

47 egg-bearing females from Kansas averaged 4.95 ± .21 (2 to 8) eggs.

21 egg-bearing females from México and Arizona averaged 7.00 ± .34 (4 to 10) eggs.

The southern females averaged markedly larger and number of eggs per clutch was closely correlated with size (Table 1). Northern and southern females of similar size produced similar numbers of eggs.

Table 1. Correlation of Snout-vent Length with Numbers of Eggs in 65 Gravid Females of *Holbrookia maculata.*

Snout-vent length in mm of females in sample	Number of females in sample	Average number of eggs, and range in sample
66-70	1	9.0
61-65	3	8.0 (6 to 10)
56-60	10	7.2 (4 to 9)
51-55	27	5.9 (4 to 9)
46-50	17	4.24 (2 to 5)
41-45	2	2.50 (2 to 3)

Holbrookia propinqua.—Selander, Johnston, Wilks, and Raun (1962:309) observed courtship and mating of these lizards on the barrier islands of the Tamaulipan Coast in northeastern México on July 6 to 10, 1961. Several females examined were found to have eggs in their oviducts.

Holbrookia texana.—In a population study of the greater earless lizard near Kerrville, Texas, Cagle (1950:230) concluded that females lay several clutches per season and that young attain sexual maturity in the first year of life. Johnson (1960:297) made an intensive study in Tarrant County, Texas; he dissected 208 females collected at different times of year and found that the average clutch has 5.0 ± .06 eggs, that females may be carrying oviducal eggs at any time from about mid-March to mid-August, and that within this period 39.9 per cent of the adult females possess oviducal eggs. On the basis of counts of corpora lutea, which steadily increased through the spring and summer, Johnson concluded that the quota of eggs for a female that survived the entire season was 25, in five clutches. Within the spring and summer breeding season adult females normally had either oviducal eggs or enlarging oöcytes indicating a continual cycle of reproduction. The proportion of adult females that carried oviducal eggs, amounting to approximately 40 per cent, implies that the cycle between ovipositions is approximately 30 days, with oöcytes attaining their full growth in about 18 days and remaining in the oviducts about 12 days. In 24 females that I examined from Texas and New Mexico there was an average of 5.32 (2 to 7) eggs.

Iguana

These are giant herbivorous lizards of México and tropical Central and South America, characteristic of riparian situations in subhumid environments and also occurring in rain forests. Nevertheless there seems to be a well defined annual cycle with a fairly restricted breeding season.

Iguana iguana.—Alvarez del Toro (1960:89) wrote that in Chiapas the breeding season is from October to December and the iguana lays its eggs in March or April. He stated that the female returns to the nest from time to time during at least the first fifteen days of incubation. The eggs hatch after approximately 90 days. Hirth (1963b:614) studied the natural history of the species at Tortuguero, Limón Province, on the northeast coast of Costa Rica, and found that egg-laying occurs in March and early April, the hottest and driest part of the year. Gravid females leave the forest to congregate on the beach where conditions are favorable for laying. Clutches consist of 29 to 40 eggs. The breeding season is timed so that hatching occurs at the beginning of the summer rainy season. Hatchlings were found emerging on June 6. In Panamá, Hallinan (1920:45) found eggs on February 24, and Swanson (1950: 187) found that eggs are laid from early February to March. Hirth cited a record by Carr of a nest found on a sandbar in Nicaragua on April 4. Copulation has been observed in autumn.

Rand (1968) studied the nesting habits on an island 60 yards long separated from Barro Colorado Island, Canal Zone, by a 20-meter channel. An estimated 150 to 200 females migrated to the island by swimming the channel for egg-laying beginning about the end of January and ending the first week of March. "Presumably breeding is timed so that the incubating eggs have the maximum insolation during the dry season [December to April] and the hatchlings have an abundant supply of herbaceous vegetation." Hatching occurred about the beginning of the rainy season—the last week of April or the first week of May. Nesting was so concentrated on the small part of the island that was suitably open, that the females excavating their burrows often dug out each other's eggs.

Breeding cycles undoubtedly are modified to some extent by local climatic conditions. In British Honduras, Neill and Allen found "babies" in April. In British Guiana, Beebe (1944:203) reported a nest with four eggs estimated to have undergone one-third of their incubation on September 26, 1922, and another nest with seven eggs was found on October 3, 1920. The clutches of four and seven eggs reported by Beebe are remarkably small as compared with those mentioned by other observers, and may not have been complete. For seven clutches reported by Hirth, and one each by Carr and Hallinan and two by Rand in Central America eggs numbered 24, 29, 33, 34, 34, 35, 36, 39, 40, 41, and 45, average 35.5. The seven females recorded by Hirth were 340 mm snout-vent and were thought to be recently matured individuals laying eggs for the first time. Much larger and presumably older individuals had been reported but were rare because of persecution by humans and dogs.

Licht and Moberly (1965:515) experimented with incubating eggs and divided a clutch of 41 into three groups, which were kept at different temperatures—20°, 30° and 36° C. Only those kept at 30° developed normally.

Laemanctus

These medium-sized, arboreal casque-headed lizards inhabit lowland forests in México and Central America.

Laemanctus longipes.—Duellman (1963:235) reported that a female from southern El Petén, Guatemala, contained four ova 13.9 mm long—probably

almost ready to be laid. In the same area five eggs were found on June 30. They were kept, and hatched on August 30. McCoy (1968:676) mentioned a clutch of three eggs.

Laemanctus serratus.—Alvarez del Toro (1960:83) stated that a clutch of three or four eggs is laid in June or July. In the Gómez Farías area of Tamaulipas, México, Martin (1958:57) found two gravid females excavating nest burrows for the reception of their eggs on June 16, 1953. Martin noted that a large female taken on January 1 had small ovaries and oviducts but enlarged fat bodies. Another female taken on March 4 had oöcytes 3.5 mm in diameter, and also had enlarged fat bodies. Eight of ten other adult females collected from late April to July had large oöcytes or oviducal eggs. Hatchlings were noted on August 28. McCoy (1968b:676) mentioned clutches of 3, 5, and 5 eggs.

Liocephalus

These are medium-small, West Indian, terrestrial iguanids. Evans (1953: 51) studied social behavior and territoriality in a confined group of *L. carinatus* received from Bimini. He observed courtship and copulation in March.

Liolaemus

Schmidt and Inger (1957:118) stated that viviparity is found in ". . . certain species of smooth-throated iguanids (genus *Liolaemus*) living in the Andes Mountains of southern South America. Presumably by retaining the developing eggs, the females of these live-bearers will keep the eggs warmer than they might otherwise be, simply because the females themselves must seek out warm situations. In their habitats it would be difficult for these lizards to lay their eggs in a place that would be sufficiently exposed to be warm by day but not so exposed as to become dangerously cold at night." This statement applies especially well to *L. multiformis.* However some other species, living under less rigorous climatic conditions, have retained oviparity. *L. multiformis* occurs at altitudes up to more than 15,000 feet in the northern Andes, and was studied by Pearson (1954:114) in southern Perú. He found that there is a distinct annual breeding cycle. Beginning in early March (autumn) follicles undergo a gradual enlargement for about two months before ovulation occurs. Embryonic development, in the oviducts, requires five to seven months and the young are born in September, October and November. By the following April (the breeding season) these young are halfgrown. They mature in time to breed in their second year. In 20 gravid females embryos or enlarged ovarian follicles averaged 5.8.

Donoso-Barros (1966) has given excellent accounts of the many Chilean species. In general these lizards inhabit open, arid areas, some in desert or scrub, others above timberline in the Andes, and still others in the severely cold climate of far southern Chile, even beyond 50 degrees south latitude—farther south than any other reptiles occur. Most are viviparous including *L. alticolor, altissimus, bibronii, buergeri, cyanogaster, darwinii, dorbignyi, fitzingerii, gravenhorstii, kingii, leopardinus, lineomaculatus, magellanicus, multiformis, nigroviridis, ornatus, pantherinus, pictus, schroderi* and *signifer.* All

the far southern and high montane species are viviparous. Oviparous species include *L. fuscus, lemniscatus, monticola, nigromaculatus,* and *tenuis.* In *L. monticola,* at least, embryos are already well developed at the time the eggs are laid. Breeding generally occurs in August or September, eggs are laid in October or November and births occur in January or February. Numbers of eggs or young recorded are: two in *L. magellanicus,* two or three in *L. fuscus* and *lineomaculatus,* three or four in *L. monticola,* five or six in *L. gravenhorstii* and about six in *L. tenuis.*

Ophryoessoides

These small iguanids of South America are similar to *Liocephalus* of the West Indies. Osorno (1938:200) observed *O. ornatus* near Bogotá, Colombia. He stated that the eggs, only two per clutch, are laid in wet ground, and that incubation requires about six months. He noted that the lizards sometimes remain underground for periods of weeks.

Phrynosaura

These are small, relatively slow-moving, coarse-scaled insectivorous iguanids of South American deserts, showing extreme xeric adaptation in their morphology comparable to that of the agamid *Phrynocephalus.* Three species are known. Donoso-Barros (1966:347) wrote that *P. reichei* of the Tarapaca Desert in Chile is oviparous; a female contained two spherical eggs.

Phrynosoma

The horned lizards are medium-sized or small, spiny-scaled flattened and squat-bodied, myrmecophagous iguanids of arid regions in the western United States and Mexico. There are both oviparous and viviparous species. The viviparous *P. douglassi* is especially characteristic of high altitudes and high latitudes.

Phrynosoma asio.—Alvarez del Toro (1960:96) wrote that in Chiapas this lizard lays its eggs, a clutch of seven to 15, in the rainy season in September or October, and they require approximately 80 days of incubation. Davis and Dixon (1961:43) found a pair copulating near Chilpancingo, Guerrero, on June 26. On August 13 the female of this pair, which had been kept, died in ovipositing and her clutch totalled 21 eggs.

Phrynosoma coronatum.—Shaw (1952:72) wrote that a female in the San Diego Zoo laid 10 eggs on June 15 and these hatched after 63 days. Another female laid a clutch of 21 eggs on June 4 and hatching occurred after 67 days. Stebbins (1954:257) noted from six to 16 eggs, average 11, in seven females from southern California and Baja California.

Phrynosoma cornutum.—The Texas horned lizard is oviparous. Van Denburgh (1922) cited statements by Strecker that: "The usual number of eggs deposited by this species is 24," and ". . . dozen or more [clutches] have passed through my hands and in every instance but one the eggs were 24 in number." Although later records have not borne out the statement that the

clutch consistently has 24 eggs, an average of only a little less, 22.5, is obtained for 13 clutches, as follows: 37, 27, 24 (Van Denburgh, 1922), 20 (Ramsey, 1956:239), 14 (Hewatt, 1937:234), 18 to 29, average between 22 and 23 in eight clutches (Stebbins, 1954:256). Copulation has been noted on April 22 in the Tularosa Basin of New Mexico by Lewis (1950:9), and by Hewatt on April 19, 1936. In the latter instance the female oviposited on June 2. Kauffeld (1943:345) noted egg-laying in mid-July in southern Arizona. At Fort Worth, Texas, Ramsey noted that young appeared each year from mid-August to mid-September. The span of several weeks indicated for the breeding season suggests that a female may produce more than one clutch per season, but direct evidence is lacking.

Phrynosoma douglassi.—This short-horned species is by far the most northern of the genus, and occurs at high altitudes over most of its range. In conformance with a trend in reptiles of high altitudes and northern climates, it has assumed viviparous habits. Stebbins (1954:260) wrote that 13 females from Arizona, New Mexico and Oregon contained 8 to 31, average 16 to 17, eggs; he recorded birth of a litter of 10 on August 27 to a Utah female, and birth of a litter of 7 on August 7 to an Oregon female. Thirteen litters recorded in the literature (Dammann, 1949b:144; Smith, 1941:114; Tanner, 1942:60; Tanner, 1954:94; Woodin, 1953:287; and Gehlbach, 1965:288) averaged 13.8 (6 to 30) young. Douglas (1966:731) recorded recently born young August 5, 6, 14, 21, and 30 in the Mesa Verde Park area of southwestern Colorado. Dates of birth in confinement are: July 5, July 20 and July 25 for Arizona material; June 25, July 11, July 20, August 3, August 10 and August 14, for litters from females in northwestern New Mexico (Zuni Mountains) and for litters from Utah females, August 14, August 16, August 24, and August 26.

Phrynosoma m'calli.—Stebbins (1954:261) recorded unlaid clutches of 7 and 10 eggs, the former with the eggs 6 to 7 mm in diameter on April 24, and the latter fully developed (8 × 14 mm) on May 14. Wood (1936:70) recorded a clutch of 28 eggs laid by one of the lizards on July 18, 1933. As the lizard was said to have been sent from Tucumcari, New Mexico (far outside the natural range) there is perhaps some doubt regarding its identity. Norris (1949:180) recorded that a female contained seven large eggs on May 15, 1948.

Phrynosoma modestum.—This is a small species of the Chihuahuan Desert and little has been written concerning it. In the Chisos Mountains of trans-Pecos Texas, Minton (1959:40) observed copulation on May 13 and observed a hatchling on July 3. At the Río Conchos in Chihuahua, Smith, Williams and Moll (1963:212) recorded a hatchling on August 25, and in the Tularosa Basin of New Mexico, Lewis (1950:9) recorded a hatchling on August 21. Bundy, Meyer, and Neess (1955:312) recorded that a female from the Carrizozo Malpais of New Mexico laid nine eggs on July 21.

Phrynosoma orbiculare.—In Morelos, Mexico, Davis and Smith (1953:102) found 12 and 13 large ova (9 mm) in two adult females of 63 and 74 mm snout-vent length, collected August 8 to 20. In the same period four immature individuals of 39 to 50 mm snout-vent length, probably first-year young, were also collected. Presumably this species, a close relative of *P. douglassi,* is also viviparous.

Phrynosoma platyrhinos.—Stebbins (1954:259) found six to nine eggs (average between 7 and 8) in ten females examined, and he concluded that most egg-laying occurs in June and early July. Shaw (1952:72) wrote that a female laid 10 eggs on June 13.

Phrynosoma solare.—Blount (1929:329) found that ovulation occurs from July 19 to August 10. Schonberger (1945:53) recorded a clutch of 28 eggs and William S. Parker (MS) recorded a clutch of 23, but usually there are fewer. At Phoenix, Arizona, Parker (MS) found that hatchlings appear in September and October. He concluded on the basis of growth rates that sexual maturity is probably reached in the second year. He found an average of 20.5 (17 to 25) eggs in six clutches.

Phymaturus

This genus contains only *P. palluma,* a squat, heavy-bodied, medium-sized, viviparous, Andean iguanid of largely vegetarian habits. Donoso-Barros (1966: 352) reported a litter of four young.

Plica

This is a South American genus. In British Guiana Beebe (1944:207) recorded a female of *P. plica* containing two eggs on May 13, 1924. In the same region Beebe (1944:208) found *P. umbra* to be "in full breeding condition" in April, May and October. He recorded a mating pair on September 9, 1919; a captive female laid two eggs on October 14, 1920. There was a wide size range in sexually mature individuals, as some, at least, attained sexual maturity at a remarkably small size compared with that of average adults.

Polychrus

The long-legged lizards are arboreal forest dwellers of tropical America. They are oviparous. In British Guiana, Beebe (1944:211) found individuals of *P. marmoratus* "in full breeding condition" in January, July, and August. On January 1, 1921, a female was found to contain seven eggs and on August 13, 1922, one was found to contain eight eggs. An extended breeding season is indicated.

Sauromalus

The chuckwallas are large, chunky, saxicolous, oviparous iguanids that occur in certain desert regions of the southwestern United States and northwestern México.

Johnson (1965:12) studied a population of S. *obesus* in the western Mojave Desert of Kern County, California. Egg-laying was observed in nature on June 22, 1960. Of 19 adult females examined in early summer, five had enlarged ovarian follicles, one had seven oviducal eggs, and the remaining 13 seemingly were nonbreeders. Hence, Johnson hypothesized that two or more years are required to complete an ovarian cycle. Shaw (1952:72) noted that a female in the San Diego Zoo laid ten eggs on August 1. Another died with

eight eggs in her oviducts on August 12. Johnson found that aestivation occurs in late summer when the succulent vegetation required as food by these lizards is scarce. The time required to attain sexual maturity is unknown, but is probably several years judging from the slow growth rate shown by several of Johnson's marked individuals that were recaptured. The reproductive potential is therefore lower than in most lizards.

Sceloporus

This large genus occurring from Canada to Panamá and from above timberline on mountain peaks to sea level has a striking array of species groups, species, and subspecies that are ecologically diverse. Some are viviparous, most are oviparous, and some of the latter retain their ova during the early stages of embryonic development. Some of the species have a sharply circumscribed breeding season with only one clutch or litter per female per year. Others seemingly breed through much of their season of activity, and an individual female may produce several clutches or broods. In some species sexual maturity is attained in the first year of life, whereas others reach maturity near the end of their second year. Hence there are great differences in reproductive potential.

Table 2. Number of Eggs per Clutch or Young per Litter in Several Species of the Genus *Sceloporus*.

Species	Mean number of eggs or young per brood	Number of broods in sample	Source of information*
chrysostictus	2.5 ± .21	14	
clarki	12	11	Kauffeld (1943a), Stebbins (1954)
cozumelae	1.8	12	Maslin (1963)
cyanogenys	12.8	10	Smith (1939), Hunsaker (1959), Kennedy (1960), Bustard (1961)
graciosus	3.63 ± .13	57	
jarrovi	8.4	10	Zweifel (1949), Carpenter (1960b)
malachiticus	4.58 ± .42	19	
occidentalis	7.69 ± .23	51	
olivaceus	14.3	28	Blair (1960)
undulatus	6.76		Kennedy (MS)
variabilis	3.00 ± .27	18	

* Present study unless otherwise indicated.

To avoid dissociating species that are closely related and similar in their reproductive cycles, the various forms for which data are available are discussed as "species groups" following the arrangement proposed by Smith (1936:555).

Sceloporus chrysostictus Group

Sceloporus chrysostictus.—This species is the sole representative of its group. A total of 216 specimens in the University of Kansas Museum of Natural History (Fig. 2) were examined from Campeche, Quintana Roo and Yucatán, México; these provide some insight into the seasonal schedule of breeding, although unfortunately none of the collections is from the fall

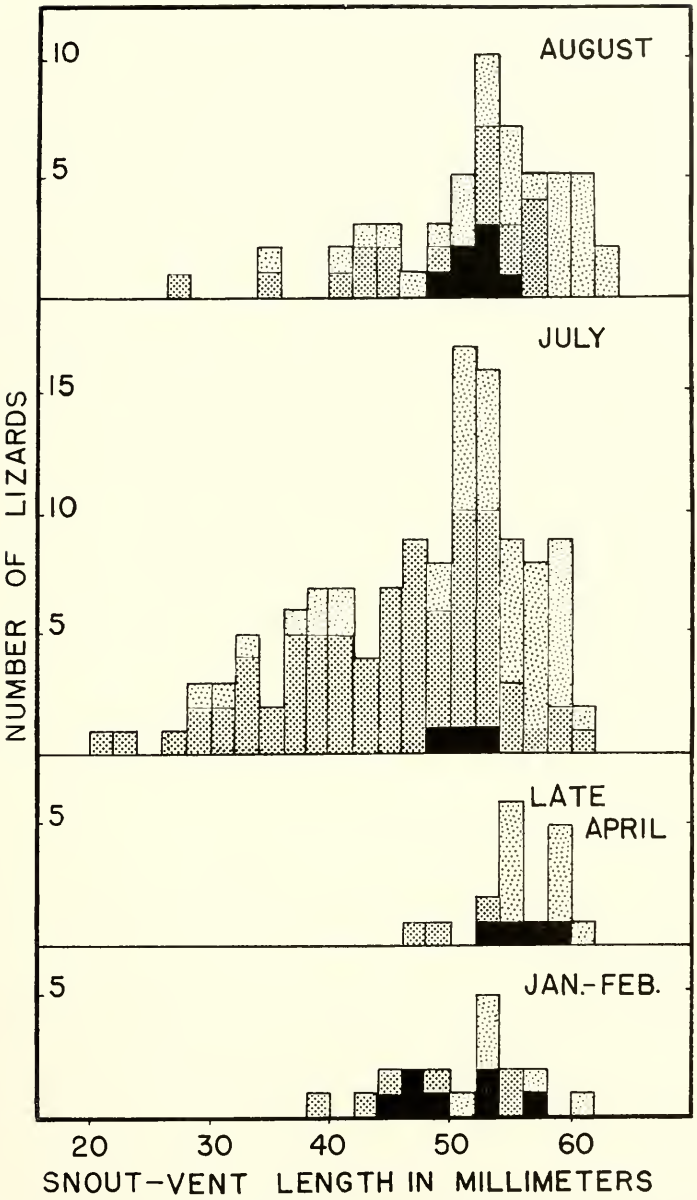


Fig. 2. Population samples of *Sceloporus chrysostictus* from Campeche, Yucatán and Quintana Roo, México, in The University of Kansas Museum of Natural History, showing changing ratios of gravid females (black), nongravid females (heavy stippling), and males (light stippling), and of adults and young. A long breeding season, extending through much of the year, is indicated, but breeding is at low ebb in July, and the ratio of young is high during that month.

months. The largest series, 125 specimens collected in July, was notable in two respects; first, that breeding was at a low ebb with only three of 47 adult females carrying eggs, and second that immatures made up nearly one-third and were of all sizes from adolescents to the smallest hatchlings. The presence of these young indicates pronounced breeding activity through the spring and early summer. In a smaller sample of 55 from August (and the first day of September) the composition had changed, with young mostly in the later stages of growth, and with nearly 40 per cent of the adult females carrying eggs. In small samples from winter (19 from January 14 to February 12) and spring (17 from April 25 and 26) a high proportion of the adult females were carrying eggs (70 per cent and 57 per cent, respectively), and young were almost lacking. Seemingly, then, the incidence of breeding is high in the winter and spring months, tapering off to a minimum in July and rising again in August and September, with perhaps a second period of reduced activity in the fall months. Compared with other species of the genus, *Sceloporus chrysostictus* carries on breeding activity for a relatively long segment of the year. However, its clutch is remarkably small as compared with most other species. In 14 females dissected the clutch averaged 2.5; one had 1 egg, six each had 2, six each had 3, and one had 4. Maslin (1963:15) recorded that four of 15 adult females collected in late June and early July were gravid, and he recorded counts of two, three and four oviducal eggs. In central El Petén, Guatemala, Stuart (1935:45) reported that hatchlings appeared on May 20 after the first heavy rain of the year.

Sceloporus formosus Group

Sceloporus cryptus.—This is a recently described species (Smith and Lynch, 1967:19) from Oaxaca, México. In the type series several females had oviducal eggs in their oviducts in a condition that indicated oviparity, whereas other members of the group are viviparous.

Sceloporus formosus.—In the Chilpancingo region of Guerrero, México, Davis and Dixon (1961:43) found that in mid-June all females 56 mm in snout-vent length, or longer, were gravid. The smaller individuals had 3 or 4 ova; the larger, 8 or 9. Smith, Smith and Werler (1952:255) recorded a female in Veracruz, México, that contained six embryos in November.

Sceloporus malachiticus.—This medium-large viviparous species occurs at the southern end of the geographic range of the genus and is present over a wide range of altitudinal and climatic conditions. Doubtless the breeding schedule is affected by local conditions. In Alta Verapaz, Guatemala, Stuart (1948:54) recorded juveniles at an altitude of 1410 meters in mid-May. Of 11 females that I collected in February in Costa Rica, all were gravid; young from hatching size (26 mm snout-vent) up to more than halfgrown size were present indicating many weeks of growth. Hence, young were being born in December and January and females producing them must have been gravid in October and through late fall and winter. The only adult female collected in April was not gravid, and no adult females were taken in May. One of the two taken in June was gravid. Of 16 adult females in June and July all but one were gravid. A young female of only 47 mm snout-vent in July also was gravid. This individual must have been still in her first year of life, probably

not more than three or four months old. Numerous young from only a little above hatchling size up to adolescents were present in the July-August sample, indicating that there must have been gravid females in the spring and early summer months, a period inadequately represented by the collections. In brief, the evidence indicates a high incidence of breeding throughout most of the year. Young females mature and produce first litters while still far short of adult size. The high percentage of females carrying eggs in each sample suggests that litters are produced in rapid succession. For 20 clutches the average was 4.5 eggs. Most gravid females are between 70 and 80 mm snout-vent. As in most reptiles, size and age of the female is an important factor in determining the number of eggs in her clutch. In the seven smallest gravid females, those with snout-vent lengths less than 70 mm the average clutch was 2.8; in 12 females having lengths of 70 to 79 mm the average clutch was 4.8; in one female of 83 mm there were six eggs, and the largest female, 90 mm in length, had nine eggs. In Guatemala, Stuart (1951:57) reported that females taken in early April were not gravid but those collected in early July contained mature eggs.

Sceloporus graciosus Group

Sceloporus graciosus.—The sagebrush swift, the sole representative of this group is oviparous and occurs in the western United States, where it ranges much farther north than most other members of the genus. In a series of 226 from the northern part of the range (Washington, Oregon, and Idaho) collected in May, June, and July, there are three overlapping size groups distinguishable: 1, old adults more than 54 mm in snout-vent length; 2, young adults, 48 to 54 mm in snout-vent length comprising the greater part of the breeding population, and 3, young hatched the preceding summer, mostly more than one quarter grown but still short of small adult size. In May all of nine adult females were carrying eggs. In June eight adult females were carrying eggs, but two collected on the 17th and 26th of the month had already laid. Of 21 adult females collected in July, only one (taken on the 26th at an altitude of 4500 feet) was carrying eggs. In southwestern Oregon and extreme northern California females are gravid in May and June, and young hatch in late July and early August. In a collection from northern California, four of six females taken in late May and June were gravid. A series of 55 from northern California in July (mainly the latter part) and early August consisted of three fairly distinct size groups: 1, breeding adults, having snout-vent lengths of 51 to 61 mm; 2, one-year-old adolescents having lengths from 45 to 49 mm; 3, recently hatched young of the year having lengths of 26 to 36 mm. Winters are long and severe in this part of the range, and a little more than half the year is spent in hibernation. In the southern part of the range (southern California and northern Baja California) the potentially longer growing season seems to have little effect in altering the breeding cycle. In a series collected in April, May, and June, 25 of 30 adult females were gravid; the exceptions were two collected on April 10 before their eggs had developed, and three others taken on June 22 (2) and June 30 after they had laid. In this series there are two size groups—breeding adults of 51 to 65 mm snout-vent length, and young recently emerged from their first hibernation, 30 to 49 mm in length but chiefly in the range of 40

to 46 mm. The two smallest individuals, both 30 mm, were collected in April, and had made but little growth since hatching.

There is no evidence of production of successive clutches by females of *Sceloporus graciosus* within one season; seemingly one clutch per adult female per year is the rule. The clutch size is relatively small; for 58 gravid females there was an average of 3.82 eggs. Clutch size is seemingly subject to some geographic variation, as 32 clutches from the northern part of the range—Washington, Oregon, Idaho, Nevada, and northern California—had an average of 3.6 eggs, whereas 25 clutches from the southern part of the range—southern California and Baja California—averaged 4.24 eggs.

Sceloporus grammicus Group

Sceloporus grammicus.—This is a widely ranging and geographically variable species which occurs from southern Texas to central México. Mulaik (1936:72) observed the species in the lower Rio Grande Valley near Edinburg, Texas. He reported seeing courtship activity on October 7, 1935, and observing gravid females in fall and early spring. A female captured on April 11 gave birth to a litter of 12 young on April 25. Gravid females collected by Werler (1951:38) at an elevation of 7500 feet in the mountains of Veracruz gave birth to litters on the following dates in 1960: January 11; February 7, 12, 16, 18, and 25; and March 6. Numbers of young per litter varied from four to seven and averaged 5.7. In Morelos, México, Davis and Smith (1953: 104) found females carrying eggs in early August. These gravid females varied in size from 33 to 67 mm. Near Chilpancingo, Guerrero, on June 9 and July 2, Davis and Dixon (1961:46) found three adult females none of which was gravid, and in early July they found partly grown young indicating a spring breeding season.

Data available are insufficient to show whether S. *grammicus* has a limited breeding season that varies from one region to another in response to local climatic conditions, or whether, as seems more probable, the breeding season is long, extending over much of the season of activity. The group includes only one other species, which is of more southern distribution.

Sceloporus merriami Group

Sceloporus merriami.—This small species of southern Texas and northern México is the sole representative of its group. Minton (1959:42) found that in the Big Bend region of Texas, hatchlings begin to appear about mid-July and at that time the remainder of the population consists almost entirely of breeding adults. Hence it seems that sexual maturity is attained in the first year of life. Chaney and Gordon (1954:78) obtained evidence that there may be more than a single clutch produced by a female in a season.

Sceloporus pyrocephalus Group

These are oviparous spiny lizards of western México. Near Chilpancingo, Guerrero, Davis and Dixon (1961:46) found that in June most adult females of S. *gadoviae* contained three or four large ova. In the same area these authors noted that most females of S. *pyrocephalus* had deposited their eggs

by mid-June, but Smith had reported females containing eggs on July 5 and 21, hence production of second clutches seemed probable.

Sceloporus scalaris Group

This group includes four species of small, terrestrial, lizards found chiefly at high altitudes in México. Davis and Smith (1953:102) collected a series of S. *aeneus* in the state of Morelos in the last week of July and the first week of August. Ten of these females had large ova; 12 others appeared to have oviposited recently, and the remaining six had small ova. Likewise, for S. *scalaris* Anderson (1962:162) found that a series of females examined from the Arroyo Mesteño at 8500 feet altitude in Chihuahua, on July 8, 1960, and June 3 to 6, 1957, were mostly gravid, with large eggs, but others appeared to have laid recently. One female was found finishing her nest after depositing her eggs under a board on July 8, and the eggs hatched 47 to 48 days later. Stebbins (1954:235) recorded a female collected in the Chiricahua Mountains of southern Arizona on July 6 that contained 9 eggs approximately 7 × 11 mm, and another from the Valley of México that contained 12 ova 3 mm in diameter on July 17.

Sceloporus siniferus Group

This group includes four Mexican and Central American species; little has been recorded concerning their reproduction. Alvarez del Toro (1960:101) stated that in Chiapas, S. *carinatus* oviposits in June or July and the clutch is seven to 10 eggs. Davis and Smith (1953:104) recorded a hatchling of S. *ochoterenai* in Morelos on August 12. Davis and Dixon (1961:46) near Chilpancingo, Guerrero, found all females to be gravid in June, with an average of six eggs. In the same area they found that in June and early July all females of S. *siniferus* were gravid and young of the year had not yet appeared.

Sceloporus spinosus Group

This group of nine large species inhabits arid regions in the southwestern United States and México. Several of the species are wide-ranging and have recognized subspecies. The group includes both oviparous and viviparous species. Eggs per clutch or young per litter are relatively numerous in these lizards as compared with other groups.

Sceloporus clarki.—Kauffeld (1943a:345) recorded that a female Clark's spiny lizard from southern Arizona contained 24 eggs with embryos 4½ to 5 mm long on August 6. Stebbins (1954:239) recorded 8 to 14 (average 11) large ova in four Arizona females collected on July 15 and 16. He recorded that a female from the Chiricahua Mountains laid 22 eggs containing well-formed embryos on September 3.

Further information concerning the extent of the breeding season is provided by 97 specimens of S. *c. boulengeri* in the University of Kansas Museum of Natural History from Sinaloa, Chihuahua, and Durango. In this series egg-bearing females were represented as follows: none (of four) from February 2

to March 8, two (of seven) in May and June, one (of 13) in September, none (of one) in October, one (of four) in November, none (of two) in December. None of two *S. c. clarki* females from Arizona in April and none of four from Arizona in August was gravid. These few records indicate that breeding extends over much of the year in *S. clarki*—at least from May to November. The smallest gravid female was only 73 mm snout-vent, whereas the largest female was 120 mm, and hence many times the bulk of the smallest. Presumably the smallest egg-bearing females are still in their first year. Probably adult females produce more than one clutch per season. Gravid females examined by me contained 10, 10, 10, 7, and 4 eggs.

Sceloporus horridus.—Davis and Smith (1953:103) recorded that in Morelos all females taken in late July and the first ten days of August contained enlarged ova while those examined in mid-August either had fully developed ova or had recently oviposited. Four newly hatched young were seen in the period August 4 to 16. In this summer period all others seen were 75 mm or more in snout-vent length—above minimum adult size. Seemingly sexual maturity is attained in the first year, and the breeding season extends over only a small part of the year. Nevertheless, there is a strong possibility that females produce two or more clutches in one season. Near Chilpancingo, Guerrero, Davis and Dixon (1961:46) found that breeding occurs from May to September. Larger and older females had an average of 12 (9 to 15) eggs whereas smaller individuals averaged nine (8 to 15). Some having enlarged oviducts indicative of recent laying also had embryonic ovarian follicles.

Sceloporus magister.—Axtell (1959:99) recorded that a female desert spiny lizard from Brewster County in southwestern Texas contained three large infertile ova on June 30 and another contained 11 follicles just beginning to develop. In the same general area Minton (1959:41) observed that there were three distinct size groups: ". . . one of about 50 mm body length and clearly young of the previous summer, one of 70-75 mm apparently individuals a year older and still immature, and finally adults of 95 mm or more." He recorded a hatchling of 33 mm snout-vent on July 19. Smith, Williams, and Moll (1963:212) reported juveniles near hatchling size in late August and early September at the Río Conchos in Chihuahua, México. Taylor (1936: 484) reported that a female from Sonora, México, contained 19 "well-developed" eggs on July 9. Shaw (1952:72) reported a clutch of *S. m. magister* laid on May 30 and clutches of *S. m. rufidorsum* on May 12, June 18, and June 27. Incubated under artificial conditions the first three of these clutches hatched after periods of 82, 77, and 61 days. Stebbins (1954:238) recorded California females with large eggs nearly ready to be laid on May 22 and June 11, and recorded clutches laid in captivity by females from Baja California and San Diego County, California, on May 12, May 30, and June 18 with incubation periods of 82 and 77 days. In eight clutches of eggs reported in the literature, number varied from seven to 19 and averaged 12.4.

In general the evidence indicates a breeding season beginning in spring but extending into early summer, with individual females probably producing successive clutches of eggs. Minton's interpretation of the three size groups in early spring, comprising adults and first-year and second-year young is undoubtedly correct, but probably the second-year young usually attain sexual

maturity and breed before they have reached an age of two years. Johnson, Bryant and Miller (1948:265) in the Providence Mountains of southeastern California noted only two size groups in May and June: adults 84 to 111 mm in snout-vent length (in 22), and young measuring 77, 71, 69, 60, 54, and 51 mm. Each of five adult females taken in this same period contained developing eggs, and these measured from 4.4 to 13.2 mm in different individuals.

Sceloporus melanorhinus.—Near Chilpancingo, Guerrero, Davis and Dixon (1961:45) found that in June adult females had five to eight enlarged ova. Alvarez del Toro (1960:97) stated that the female lays 15 to 20 eggs in June.

Sceloporus olivaceus.—Through the work of Blair (1960) in the vicinity of Austin, Texas, the general ecology and reproduction of this species are better known than for any other member of the genus. The breeding season is long, continuing over much of the warmer half of the year when the population is continuously active. Both the number of eggs per clutch and the number of clutches per season vary according to the age and size of the female. The females from eggs hatched one summer mature some time in the following summer, but one clutch per season is typical for newly matured females, and on the average, first clutches have 11.3 eggs. Two-year-old females have made additional growth, and usually produce more eggs per clutch than first-year individuals and more than one clutch in the season. The largest females (four-year-olds, rarely even older) may produce as many as 100 eggs (four clutches of about 25 eggs each) in a season. Over a five-year period Blair calculated that 945 clutches with a total of 15,080 eggs were produced on his ten-acre study area, and the average clutch was 14.3 eggs. Percentages of the total number of clutches that were produced by first-, second-, and third-year females were 46.2, 41.3, and 12.5, respectively.

Sceloporus orcutti.—Mayhew (1963) made a four-year study of reproduction in the granite spiny lizard in the vicinity of Riverside in southern California. He found that testes are relatively small at the time of the lizard's emergence from hibernation in January and February, but grow to the maximum size in April, then decline from May to August. Males appear to be potential breeders (having motile sperm in the vas deferens) from mid-March to mid-August. In females ova accumulate yolk in late April, and there are eggs in the oviducts from late May to late July, with an average of 11 per clutch. Mayhew suggested that the relatively short season during which females have eggs in their oviducts indicated only one clutch of eggs laid per year, but hatchlings appeared over a two-months period, July 30 to September 27. Reproductive success varied greatly from year to year, evidently in response to the amount and distribution of rainfall in this arid region.

Sceloporus torquatus Group

This large group contains ten species, several of which have recognized subspecies. These lizards are relatively large; insofar as known, all are viviparous. In most lizards of the Temperate Zone, including *Sceloporus* and including both oviparous and viviparous species, the young characteristically appear in late summer, but in the species of this group the young are born in early summer, late spring, or even in late winter.

Sceloporus cyanogenys.—Hunsaker (1959:261) recorded that seven females collected in Webb County, Texas, on March 15, 1958, each gave birth to a litter in the subsequent period of weeks that the lizards were kept. Size of female (snout-vent in millimeters), number of young per litter, and dates of birth were as follows:

88	6	May 31
98	12	May 21
99	12	May 14
104	12	June 5
106	15	June 11
125	18	May 5
126	18	May 31

Kennedy (1960:44) wrote that a female of 108 mm snout-vent length taken near Laredo, Texas, gave birth to 17 young on February 28, 1959. Smith (1939:223) recorded that one from Rio Grande City, Texas, bore 11 young on June 2, 1937. Bustard (1961:217) reported birth of a litter of 13 on June 12-14.

Sceloporus dugesi.—Smith (1936:661) reported that in early June in Nayarit and Jalisco, México, newborn young were seen in abundance, and adult females at that time had no eggs in their oviducts. He stated that hatchlings of *S. d. intermedius* were frequently collected in August.

Sceloporus jarrovi.—Carpenter (1960b:137) recorded birth of young Yarrow's spiny lizards from females collected in the Huachuca and Chiricahua Mountains of southeastern Arizona in late March. Litters of young were born on June 4, June 13 (2 litters), June 16, and June 17 (2 litters) and litters had from 7 to 13 young, average 10. The females ranged from 74 to 85 mm in snout-vent length. Zweifel (1949:152) recorded 10 young born June 27 from an Arizonan female. In Morelos, México, Davis and Smith (1953:103) found an average of five ova in females of *S. j. sugillatus,* perhaps indicating geographic variation in size of litter.

Records of 107 *S. jarrovi* examined by me from the Chiricahua Mountains, Arizona, further clarify the schedule of reproduction and growth of the species in that region (Fig. 3). Of 12 collected in April, all were sexually mature and the smallest individual, a female of only 57 mm snout-vent, was gravid, carrying three eggs. This individual and several others not much larger were evidently born the preceding summer. In a July sample, based upon measurements that I obtained from live lizards in the field, the young of the year, already well above minimum size, comprised a distinct size group well set off from the adults. The latter were themselves divisible into three size groups: newly matured adults 61 to 72 mm in length, those of typical adult size 75 to 81 mm in length in their third year or older, and old adults more than 90 mm in length. In the August sample both adults and first year young have made an increase over the average July sizes and the hiatus in size between young and adults has narrowed somewhat. Because of the long gestation period and the concentration of births in June, it is reasonably certain that a single litter constitutes the quota of each female for a year—at least in Arizona at the northern end of the species' range. The four gravid females that I examined from Arizona in April differed in number of eggs carried according to size

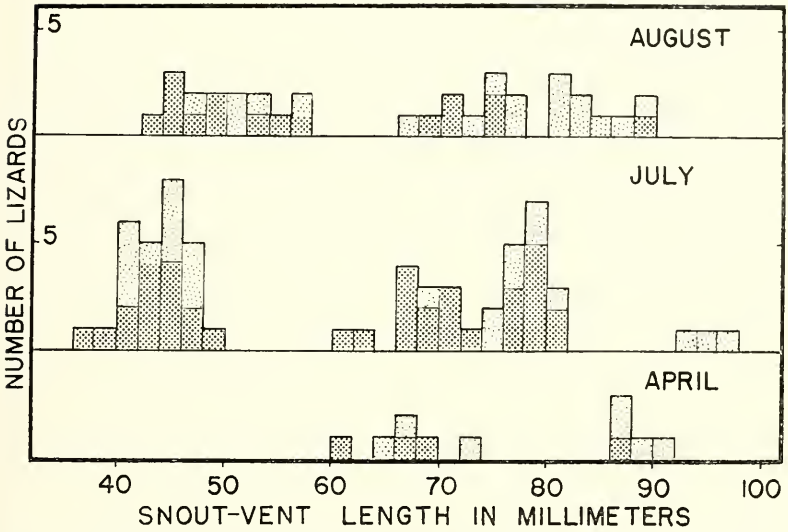


Fig. 3. Population samples of *Sceloporus jarrovi* from southeastern Arizona in The University of Kansas Museum of Natural History showing changing sizes of males (light stippling) and females (heavy stippling) at different times of year. In April the population consists of adults of two sizes: old survivors and newly matured individuals born the preceding summer. By July each of these groups has made further growth and a new crop of young has appeared. By August both adults and young have made further growth.

(snout-vent length) as follows: 86 mm—13 eggs; 68 mm—3 eggs; 67 mm—5 eggs; 57 mm—3 eggs.

Sceloporus mucronatus.—Werler (1949a:67) reported that a female from Las Vigas, Veracruz, México, produced nine young on January 6, 1949. In the same area Smith, Smith and Werler (1952:256) found six females collected from November to January all gravid, some with embryos near full term. In the vicinity of Chilpancingo, Guerrero, México, Davis and Dixon (1961:46) found that by early June breeding activity was over and young of 34 to 36 mm in snout-vent length were abundant. They speculated that the main breeding season was in March or April.

Sceloporus poinsetti.—In the Big Bend region of southwestern Texas, Minton (1959:41) noted that newborn crevice spiny lizards were first seen on July 16 to 18. In the same general area Axtell (1959:100) noted a small juvenile (42.8 mm snout-vent) on June 26. Smith (1936:612) recorded that a female taken on May 31 contained 10 well-developed embryos, and he concluded that the young probably are born early in June. Stebbins (1954:236) stated that two females from Chihuahua, México, contained seven and 10 embryos respectively, and that one from near Fort Stockton, Texas, had seven young in captivity on June 6, and another from Kimble County, Texas, had 11 young on June 7.

Sceloporus serrifer.—In central El Petén, Guatemala, Stuart (1935:45) saw

recently hatched young on May 17 and 18, just before the onset of the rainy season.

Sceloporus torquatus.—Smith (1936:576) wrote that in Zacatecas, México, young of this species are born in spring. In Morelos, México, in late summer Davis and Smith (1953:104) recognized three distinct size-age classes of which the two larger were sexually mature, and they suggested that maturity is attained in the first year of life. Werler (1951:39) wrote that a female from near Morelia, Michoacán, México, gave birth to six young on May 8, 1950.

Sceloporus undulatus Group

This group has four species and includes two of the lizards most familiar to residents of the United States—*Sceloporus occidentalis* of the far western states and *Sceloporus undulatus* of the eastern states, occurring west through the southern Rocky Mountains. S. *virgatus* is a species of southern New Mexico and Arizona and adjacent México. S. *cautus* is a Mexican species for which no information is available. Because much information is available from different areas of the ranges of the other species and because there is evidence that reproductive cycles are subject to some alteration in response to the physical and biotic factors that occur in different regions, the subspecies will be considered individually insofar as data are available.

Sceloporus occidentalis biseriatus.—This relatively large subspecies occurs in the southern and eastern parts of the range—from the Columbia River in Washington and Idaho south through the Sierra San Pedro Martir in Baja California. Hence, its populations occur in rather diverse climates, but there is little evidence of major change in seasonal cycles in different regions. In the northern part of the range the population is subjected to a severe winter climate, and the growing season is short, probably only about half of the year. At the southern end of the range, the winter climate is mild and hibernation must be short and intermittent. In the foothills of the southern Sierra Nevada, where I had the opportunity to observe these lizards over a period of years (at the San Joaquin Experimental Range in Madera County, California) there was some activity throughout the year; on warm sunny days, even in December, January, and February lizards would emerge to bask, and probably to feed.

A series of 46 in the Museum of Vertebrate Zoology from the northern part of the range in eastern Oregon and Idaho was examined. Size classes are not well defined in this series, but the May-June sample, of 39 specimens, is interpreted as constituting essentially two size groups: namely, adults, and young produced the preceding summer. Adults are 65 to 87 mm snout-vent, and young are 31 to 63 mm. The wide size range in the first year young is in part geographical and altitudinal. In a series of 102 S. *o. biseriatus* from 500 to 1000 miles farther south, southern California and northern Baja California, gravid females are represented as early as April 10 and as late as July 10. Such an extended egg-laying season strongly suggests that a female may produce more than one clutch, but definite proof for this supposition is lacking. In April, May, June, and July samples the young in this southern population do not comprise a distinct size group but most are in the 60 to 70 mm range —approaching adult size with some not readily distinguishable from small adults.

Thirty-seven gravid females of *biseriatus* had an average of 7.65 (3 to 14) ova.

Sceloporus occidentalis longipes.—Hopkins (MS) has studied the life history of this lizard in montane habitat on Ranier Mesa in southern Nevada. The lizards breed at an age of two years. Clutches of nine eggs each were laid by females 72 and 73 mm in snout-vent length, and clutches of 10 and 11 in females of 77 and 76 mm. An 86 mm female laid 14 eggs. Laying occurs in June and July, and hatching is in August and September. Immediately after egg-laying the females replenish their fat bodies.

Sceloporus occidentalis occidentalis.—In a five-year study of this form near Medford in southwestern Oregon and 300 miles farther south at Berkeley, California, 1 (Fitch, 1940) accumulated the following facts regarding its breeding and seasonal schedule. Mating occurs in late March or early April soon after emergence from hibernation. Oviposition occurs in late May or early June. Hatching is concentrated during the first week of August, but with extreme limits from mid-July to mid-September. Variation in weather from year to year, and variation in incubation period according to the nest site chosen and the amount of warmth received, account for most of this difference. It is unlikely that an individual female ever produces more than one clutch of eggs per season at either of the localities where observations were made. At the time of the spring breeding season first-year young from eggs hatched the previous summer are mostly 35 to 45 mm in snout-vent length, the largest far short of adult size which is typically 65 to 70 mm. Most growth is made during the subsequent summer and sexual maturity is attained late in the second year.

Fourteen gravid female *occidentalis* had an average of 7.8 ova, with a range of four to 13, hence not differing significantly from *S. o. biseriatus.*

Sceloporus undulatus consobrinus.—Carpenter (1959a:110) studied a population of this subspecies in south-central Oklahoma. He found that hatchlings appeared from mid-June through July, and comprised a size group distinct from the adults through the summer and fall, but that by the following spring they were no longer readily distinguishable from adults. Contrasting lizards of this subspecies with populations of three other subspecies that also occur in Oklahoma, Carpenter (1960:178) found an average clutch of 6.2 (3 to 8) eggs in 13 *S. u. consobrinus,* whereas there were 9.0 (4 to 13) in six *S. u. erythrocheilus,* 7.6 (5 to 12) in ten *S. u. garmani,* and 7.1 (4 to 12) in 13 *S. u. hyacinthinus.*

Sceloporus undulatus elongatus.—This large northwestern subspecies living at relatively high altitudes, with a short growing season, seemingly does not attain sexual maturity until late in the second year, at the northern edge of its range, at least. In a series of 21 collected near the Utah-Wyoming boundary, in Daggett and Sweetwater counties, respectively, June 15 to July 24, snout-vent lengths ranged from 46 to 79 mm. Those from 46 to 54 mm appeared to be yearlings (hatched the previous summer) and those from 65 to 79 mm were adults, but the status of six that measured 60 to 62 mm was uncertain.

In southwestern Colorado, Douglas (1966:727) found gravid females in June and early July, and one contained ovarian eggs 4 × 5 mm on August 5.

Douglas speculated that some females might produce a second clutch. He found an average of six eggs per clutch. In adjacent northeastern New Mexico, Gehlbach (1965:281) found that in June and up to mid-July most females over 40 mm snout-vent contained eggs. Gehlbach observed that in some females containing uterine eggs, embryonic development was well underway and the relatively large, pigmented eyes of the embryos were conspicuous. The author suggested that fertilized eggs are retained by the females for varying lengths of time, so that they can be deposited when conditions are most favorable for them—after heavy rains.

Sceloporus undulatus erythrocheilus.—Compared with its neighbor, *S. u. garmani* of the Great Plains, this subspecies is much different ecologically. It has a shorter growing season and attains a much larger size. Both facts may be correlated with the delayed sexual maturity. Seemingly sexual maturity is usually not attained until late in the second year in *erythrocheilus.* On August 15 and 16, 1964, at Black Mesa State Park in the western tip of the Oklahoma Panhandle, I observed 37 of these lizards of which two were hatchlings and the remainder were adults and subadults. Although the latter two groups were no longer well defined, some of the subadults were still markedly below average adult size and obviously would have been immature and incapable of breeding in the previous spring. In southeastern Colorado, Smith, Maslin and Brown (1965:20) first observed young of the year on August 12, 1961.

In a mid-June collection of 37 *erythrocheilus* from northern New Mexico there were gravid females 70, 69, 68, 68, 64, and 63 mm in snout-vent length, and many smaller ones assumed to be young of the preceding summer were not gravid, but a specimen only 41 mm in snout-vent length contained ovarian follicles 6 mm in diameter. In this seemingly exceptional instance breeding maturity had been attained by a first-year individual at a size much below that of an average adult, but 12 other females ranging from 35 to 62 mm snout-vent were not gravid and probably had not yet attained sexual maturity.

Sceloporus undulatus garmani.—A series of 76 in the University of Kansas Natural History Museum from various parts of Kansas indicate a long breeding season. An adult female collected on May 8 was gravid, as were ten of 15 females collected in June, all four collected in July and three of four collected in August. No specific dates are available for those collected in August. Five hatchlings 21 to 23 mm in length were collected July 2 to 14.

At a locality 17 miles west of Nickerson, in Rice County, in sand dunes near the Arkansas River, I made repeated observations on a local population in three seasons (Fig. 4). On May 3, 1966, it was found that the populations consisted essentially of adults, but with a wide range in size—from 39 to 62 mm, snout-vent. Males of 43 and 45 mm were mature and had motile sperm, and only the smallest male of the series (39 mm) had not yet matured. All but a few of the smallest females were slightly but noticeably distended with eggs. Three overlapping size groups could be postulated: 1—the young of the preceding year, including those of less than 46 mm snout-vent length (but probably others of this age group were more than 50 mm and overlapped the next group); 2—the main group, 48 to 54 mm snout-vent, mostly second-year individuals but including the more successful and older first-year young; 3—adults well above average size (56 to 62 mm) and probably more than two

years old. In a sample collected on July 11 there were only 15, but they fell into the same three size groups. All the females were gravid. In a sample collected on August 10 there were two distinct size groups—breeding adults 50 to 67 mm snout-vent, and hatchlings 25 to 41 mm. The same two discrete groups were represented on August 26, but the average size and size-range of the young had increased and the interval between young and adults had

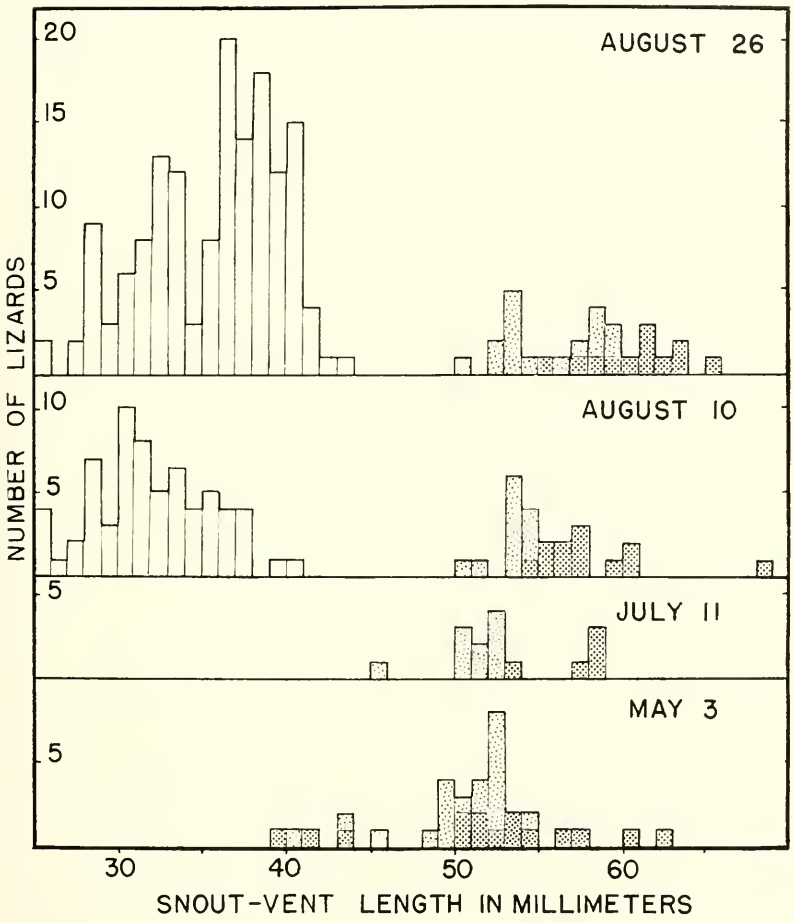


Fig. 4. Population samples of *Sceloporus undulatus garmani* from a roadside fence 17 miles west of Nickerson, Rice County, Kansas; heavily stippled columns show adult or subadult females, lightly stippled columns show adult or subadult males, and open columns show juveniles. In early May the population consists essentially of breeding adults. In early August young of the year outnumber adults and some have already made substantial growth. By late August the young of the year have increased markedly in relative abundance and in average size, with a tendency to bimodality in size, indicating first and second broods. Adults as well as young make substantial growth in the summer. Samples are based upon lizards captured alive, measured in the field, and released.

decreased markedly. Average size of adults increased from spring to late summer, as shown by the following table.

TABLE 3. Changing Size (Snout-vent Lengths in mm) in a Population of *Sceloporus undulatus garmani*, Rice County, Kansas.

Date	Adult and subadult males	Adult and subadult females	Young
May 3, 1966	49.7 ± 1.61	51.4 ± 1.87	absent
July 11, 1964	52.4 ± .71	56.8 ± .83	absent
August 10, 1964	52.8 ± .36	57.8 ± 1.03	31.0 ± .44
August 26, 1964	54.8 ± .71	60.5 ± .83	35.1 ± .32

Sceloporus undulatus hyacinthinus.—Through the studies of J. P. Kennedy (in press) near Houston, Texas, this is one of the best known lizards ecologically. With the mild winter and long growing season of the Houston region, the time of breeding is prolonged and some females produce five clutches or possibly even more in the course of a year. One laid successive clutches on: April 22, May 24, June 23, July 11, and about July 31. Growth is rapid and the young mature soon enough to breed within the first year of life—that is to say, young hatched in one summer may produce eggs of their own early the following summer. Kennedy's figures indicated that such "yearlings" usually produced either one or two clutches averaging five eggs each, whereas the two-year-olds produced three clutches of six eggs each, and the three-year-olds (a relatively small group percentagewise) produced four clutches of eight eggs each.

The climate in the Houston region in the southwestern end of the range of this subspecies is probably near the optimum for the growth and development of these lizards. Farther north in regions having longer and more severe winters, it might be expected that development would be slower, attainment of maturity would be delayed, and reproductive potential would be much

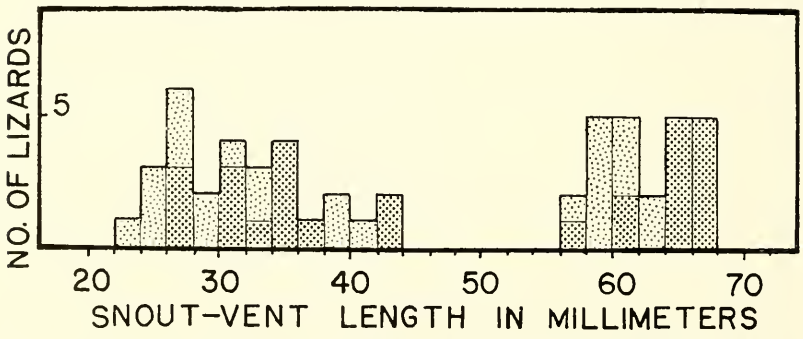


FIG. 5. Population sample of *Sceloporus undulatus hyacinthinus* from Wister Dam, Le Flore County, southeastern Oklahoma, August 17 to 21, 1966, showing females in heavily stippled columns and males in lightly stippled columns. At this time the breeding season was over, adults and young comprised distinct size-groups, and the young covered a wide size range, from new hatchlings to juveniles twice their length and obviously several weeks old. A long egg-laying season is indicated. Sample is based upon lizards captured alive, measured in the field, and released.

lower. At Wister Dam in southeastern Oklahoma, August 11 to 15, 1963, I observed large numbers of *S. u. hyacinthinus* and handled and measured many. They fell into two discrete size groups—adults, and young of the year. Some of the adults appeared to be newly matured (young of the preceding year); others were much larger and bulkier, but none of the females was gravid. Some of the hatchlings appeared to be newly emerged, judging from their small size and prominent umbilical scars, and perhaps there were still unhatched eggs in nests. Other young were several times the bulk of the smallest hatchlings, and appeared to be several weeks old. The same area was revisited August 17 to 21, 1966, and 53 of the lizards were caught and measured. Young of the year ranged in size from newly emerged hatchlings, the smallest 22 mm snout-vent, up to individuals of nearly twice this length (43 mm) which must have hatched in early July (Fig. 5).

Sceloporus undulatus tristichus.—This large southwestern subspecies seems to resemble the ecologically similar *erythrochcilus* and *elongatus* and to differ from the smaller, more eastern *garmani* and *hyacinthinus* in requiring almost two years to attain sexual maturity. In a series of 30 from southern Arizona collected from June 19 to July 19, the majority (17) were obviously immature—46 to 57 mm in length. Only the two largest in the series—68 and 74 mm snout-vent—were gravid. In a series of 14 collected in the same general area in August, adults and young of the preceding year were no longer distinguishable, and most fell in the size range 55 to 66 mm. One exception was an unusually large female of 85 mm, the other was a juvenile of 40 mm, probably a young-of-the-year already several weeks old when collected in late August.

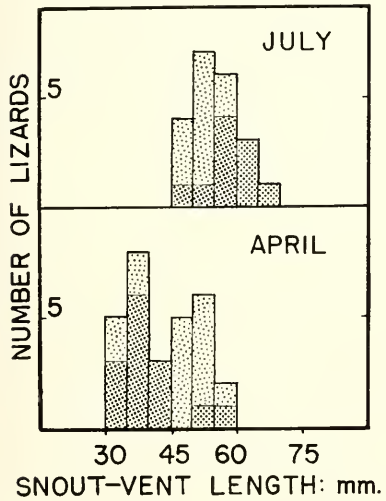


Fig. 6. Population samples of *Sceloporus virgatus* from southeastern Arizona based on specimens in The University of Kansas Museum of Natural History; females shown in heavily stippled columns and males in lightly stippled columns. In April, before the breeding season, the population consists of adults and subadults, the latter representing the preceding year's young. By late July the breeding season is completed but young of the year have not yet appeared and the adults have made additional growth.

Sceloporus undulatus undulatus.—Crenshaw (1955) made a field study of this lizard in Baker County, Georgia. In 11 clutches he found an average of 7.6 (6 to 10) eggs. Egg-laying occurred from May 2 to about the end of July, and hatchlings were found from June 21 to at least September 5; probably hatching continued into late September. The intervals of many weeks covered by both laying and hatching seemed to indicate production of two or more clutches per season, but no definite instances were recorded. Young ma-

ture in their first year. One female hatched about midsummer of 1949 was found to be gravid on April 26, 1950.

Sceloporus virgatus.—This small species, a near relative of S. *undulatus,* with which it was long included as a subspecies occurs in arid foothills and mountains in the region where Arizona, New Mexico, Sonora, and Chihuahua meet. Cole (1963:415) studied the species in southern Arizona and New Mexico and found that nearly every adult female collected in June was gravid, but that most collected after mid-July were not gravid. He found that hatching occurred in the third and fourth weeks of August in 1960 and 1961. I captured and observed many of these lizards in the Chiricahua Mountains of southeastern Arizona from July 18 to August 3, 1956. In this period none was gravid, but some appeared to have laid recently. A series of 25 collected in this same area on April 5, 6, and 7, 1963, consisted of adults, adolescents and large young, the latter two groups ranging from 31 to 43 mm in snout-vent length and representing the brood of the previous August. With several weeks additional growth, by the time of the breeding season, these smaller individuals presumably would have matured. Comparison of measurements in the April and July series shows that the average size increased from 49.0 to 55.6 mm in the interval of about 11 weeks, and that the bimodality of the April series had disappeared. S. *virgatus* resembles S. *undulatus garmani,* S. *u. hyacinthinus,* and many other members of the genus in reaching maturity and breeding before the end of the first year. However, it seemingly differs from most other warm-climate species and resembles S. *o. occidentalis* in producing only a single brood per year. Hence it is somewhat intermediate in its reproductive potential.

Sceloporus variabilis Group

Sceloporus cozumelae.—This tropical species was observed by Maslin (1963:13) on the Yucatan Peninsula of México within the period June 19 to July 12. Of 18 adult females collected, 12 were gravid, with medium-sized to large eggs. In three the eggs were uterine with shells already formed. The average number of eggs per female was only 1.8. Of the 36 lizards collected, 11 were juveniles and others were subadults, indicating that the breeding season was prolonged.

Sceloporus teapensis.—This species was observed by Stuart (1948:54) in Alta Verapaz, Guatemala. He noted newly hatched young in late August at an altitude of 675 meters.

Sceloporus variabilis.—This small species, one of the southernmost of the genus, is widely distributed in the tropics, and occurs from ocean beaches to moderately high altitudes. Populations may differ in their mode of reproduction, in response to local climates, as published accounts of different authors indicate both oviparous and viviparous habits. Stuart (1948:55) reported hatchlings in late June in Alta Verapaz, Guatemala. Alvarez del Toro (1961: 103) wrote that in Chiapas, México, the female of this species lays a clutch of four eggs at almost any time of year. The statement is unique in this author's account, and he indicated relatively short breeding seasons for most of the reptiles of Chiapas on which he had information. Brattstrom and Howell (1954:118) recorded that a female of S. *variabilis* from an altitude near 3000

feet in Nicaragua contained six oviducal eggs in January. Stuart (1948:55) reported hatchlings in Alta Verapaz in June. Werler (1951:38) wrote that a female from Veracruz at 7500 feet altitude contained seven nearly full-term embryos on February 11, 1950.

Further clarification of the breeding cycle in S. *variabilis* is provided by 130 specimens examined in the University of Kansas Museum of Natural History. Twenty-eight of these were obtained by me in Guanacaste, northwestern Costa Rica, in late March and 18 others came from the same locality in July, while the remaining specimens are from Veracruz, México, and are fairly evenly distributed between the months of January, February, April, May, October, November, and December. The March series consists almost entirely of adults, but three hatchlings were obtained and several others were seen. Only two of eleven adult females were gravid and it seemed that most of the females had oviposited recently and a breeding period was drawing to a close, with the earliest eggs already beginning to hatch. The lack of individuals of intermediate size in the series indicated an earlier period of months (fall and early winter) in which no breeding activity occurred. In the July series from Costa Rica all ten of the adult females were gravid. There were also eight adult males but no lizards short of adult size, again suggesting a prolonged pause in breeding activity, this time in the spring months. The specimens from Veracruz show the following changed ratios of females that were gravid and of immatures from month to month.

	Percentage of females that were gravid	Percentage of immatures in sample
January	33% (of 3)	29% (of 7)
February	100% (of 1)	25% (of 4)
April	67% (of 3)	14% (of 7)
May	100% (of 3)	10% (of 10)
October	22% (of 9)	29% (of 24)
November	25% (of 4)	14% (of 22)
December	100% (of 5)	20% (of 10)

Although some of these series are small the combined data suggest that some breeding occurs throughout much of the year in Veracruz.

In 18 clutches of *Sceloporus variabilis* the number of eggs averaged exactly three and varied from one to five; seemingly in the small lizards of the S. *variabilis* Group characteristic of tropical climates, the clutch size is small and is compensated by production of frequent clutches.

Tropidurus

The lava lizards of this genus occur on the mainland of tropical South America and on the Galapagos Islands. They are small, active and terrestrial. Loveridge (1945:92) stated that the breeding season of *T. albemarlensis* on the Galapagos is in May and June, and he described the gaudy coloring assumed by the females at this time. He stated that from four to six eggs are laid in burrows. A somewhat different impression of time of breeding and size of clutch is provided by the recent account of Stebbins, Lowenstein and Cohen (1967:839-851) based on the same species on the island of Santa Cruz

(Indefatigable). They found breeding to be at or near its peak during their visit from January 23 to February 27, 1964. For 54 clutches of unlaid eggs the average was 2.17, and more than two-thirds had just two eggs, but other clutches had three, one and four in that order of frequency.

Burt (1935:168) noted that a series of 15 *T. occipitalis* from La Libertad, Ecuador, collected on January 20, 1933, showed gradation in size from small young (33 mm snout-vent length) to adults. A long breeding season is indicated.

Uma

The sand lizards are small, terrestrial, oviparous iguanids confined to areas of fine drifting sand dunes in several isolated areas in southwestern United States and adjacent México. They are closely related to lizards of the genera *Callisaurus* and *Holbrookia,* and like them, have an extended breeding season with the potentiality for several successive clutches to be produced by one female.

Uma inornata.—Mayhew (1964b:49) studied the annual cycle and reproductive habits of this lizard, and found that females might have eggs in their oviducts any time from the last days of April through the first week of September. Corpora lutea could be found in females over the same period, and up to mid-September. Mayhew concluded that a female may produce more than one clutch in a season. He stated ". . . a few precocial *Uma inornata* of both sexes may breed in late summer following the year they hatch but the majority normally reach reproductive maturity during the second summer following hatching." Gravid females had two, three, or four eggs in that order of frequency. For 16 clutches the average was 2.44. In males, testis volume changes markedly as the season progresses, with the maximum attained in May. Males may breed from mid-May to mid-August.

Uma notata.—This lizard also has been studied by Mayhew (1966b) in the deserts of southeastern California. As in *U. inornata,* eggs have been found in the oviducts over a 3½-month period. Under experimental conditions in confinement females have produced successive clutches in 30 days and 39 days (Mayhew, 1964b), hence two or three clutches per season may be expected. A two-egg clutch is most typical, followed in frequency by clutches with three, one, four, and five eggs in that order. After dry winters the annual crop of vegetation is underdeveloped and its insect fauna is lacking, and under these unfavorable conditions reproduction seemingly stops. In poorly fed males testis volume remains small. As in *U. inornata* most young reach sexual maturity in the second summer after hatching, but there are a few precocious yearling breeders.

Uma scoparia.—In this species, Mayhew (1966a:114) found females with oviducal eggs from mid-May to mid-July. Extent of reproductive activity varies from year to year according to the amount of winter rainfall. After dry winters testes remain small, females have relatively few eggs in their ovaries, and there is a noticeable scarcity of hatchlings in late summer and autumn. Most lizards of both sexes reach reproductive maturity in the second summer after hatching.

Uranascodon

This is a genus of tropical South America. Beebe (1944:214) stated that a female *U. superciliosa* from British Guiana laid 11 eggs on August 5, 1920 and six on August 22, 1922.

Urosaurus

The tree lizards are small, active and scansorial and inhabit arid regions in the southwestern United States and México. They attain maturity within the first year of life, and, in some instances at least, a female produces two or several successive clutches within a single breeding season.

Urosaurus bicarinatus.—Alvarez del Toro (1960:103) reported that in Chiapas, México, the female of this species lays a clutch of 10 eggs in June. Davis and Smith (1953:105) reported hatchlings in mid-August in Morelos, México, and also stated that females collected then had enlarging ova, implying an extended breeding season and the production of more than one clutch per female.

Urosaurus graciosus.—Shaw (1952:72) reported egg-laying in confinement on May 19 and July 25 by two females from Borego Valley, San Diego County, California. These eggs hatched after incubation periods of 78 days and 61 days, respectively. The records imply an extended breeding season. Stebbins (1954:249) reported an average of four eggs in eight females.

Urosaurus microscutatus.—Shaw *(loc. cit.)* reported that females laid their clutches in confinement on June 19 to 23, and on June 27.

Urosaurus ornatus.—William S. Parker (MS) studied a population of the tree lizard at Phoenix, Arizona. He found an average of 4.8 (2 to 7) large ova in 24 females. Oviposition extended approximately from April to early September. In the males, testes began enlarging in February and reached maximum size in March in many individuals. Size of testis decreased from late August through September, and was minimal in October. By April most of the previous year's young had reached minimum adult size, and these yearlings made up the greater part of the breeding population. Hatchlings were abundant in July and August.

Asplund and Lowe (1964) studied a population in southeastern Arizona. They found that testes undergo enlargement in late spring reaching a maximum in June, then retrogress until late September. Females have large ovarian or oviducal eggs in June and early July and egg-laying is concentrated in the second week of July.

First appearances of hatchlings have been recorded on July 31 (Minton, 1959:42, in the Chisos Mountains of southwestern Texas), August 10 (Gehlbach, 1965:287, in the Zuni Mountains of northwestern New Mexico), and August 28 (Douglas, 1966:729, in Mesa Verde National Park).

My own observations based on limited field experience with populations in several southwestern states, and on examination of 558 museum specimens, extend somewhat the findings of these authors. In 30 gravid female specimens, eggs averaged 6.3 ± .337 per clutch. Clutches ranged from three to 13 eggs, but there were either 5, 6, or 7 eggs in 23 instances. The average clutch was

just the same for 14 specimens from Presidio County, Texas (*U. o. schmidti*), and for 16 specimens from southern New Mexico and Arizona (*U. o. chiricahuae, U. o. linearis*). Table 4 shows the incidence of gravid females among those examined in different months. A lengthy breeding season is indicated

Table 4. Numbers of Adult Females of *Urosaurus ornatus* Collected in Different Months and Percentages That Were Gravid.

Month	Number of adult females in sample	Percentage of adult females having oviducal or large ovarian eggs
February	5	0
March	7	0
April	44	7.3
May	32	37.5
June	60	88.4
July	51	72.5
August	7	28.6
September	3	0
October	6	0

and probably most adult females produce at least two clutches of eggs in a season. Strong evidence of repeated ovipositions was obtained by the writer in the summer of 1956 at the American Museum of Natural History's Southwestern Research Station near Portal, Arizona. A marked female was observed excavating her nest burrow on July 19 and was subsequently found thin and wrinkled after egg-laying, but two weeks later she was obviously gravid again. At Phoenix, Arizona, William S. Parker (MS) concluded that about six clutches per season were typical for fully adult females.

Urostrophus

This genus includes four oviparous medium-sized South American species. They are insectivorous and somewhat arboreal. Donoso-Barros (1966:370) wrote of *U. torquatus* that breeding is in the southern summer, January or February, the clutch of five or six eggs is buried in loose sand, and hatching occurs the following summer.

Uta

These small, terrestrial, lizards inhabit arid regions in the western United States and México.

Uta mearnsi.—Hain (1965:78) studied a population of these lizards in a desert canyon in southern California, and found that egg-laying occurs in late June and early July. No females were carrying eggs after July 4. The short time during which gravid females were found suggested that a single clutch per female was the rule. The clutch averages four eggs (2 to 6).

Uta stansburiana.—Through the studies of Tinkle and his associates in Texas the brown-shouldered lizard is one of the best known lizards eco-

logically. Tinkle (1961:206) found that sexual maturity is attained in the first year of life, and that almost all lizards are reproductive in the mating season. In field observations Irwin (1965:101) found a strong tendency toward monogamy, with male and female often in close association as joint occupants of the same area. There is an annual turnover of the population, so that few adults present in one breeding season survive to participate in the next. For those females that survive through an entire breeding season, three clutches of eggs is the normal complement. The average clutch has 3.8 eggs but large females lay more eggs than smaller ones. Also, size of clutch undergoes reduction from an average of 4.2 in March to only 2.7 in August.

William S. Parker (MS) studied these lizards at Phoenix, Arizona. There hatchlings first appeared in late May, but most emerged in June (80 per cent of sample) and they were abundant in July (25 per cent of sample) becoming scarce later in the season. In August, many young of the year attained adult size. Parker's observations confirmed Tinkle's findings in Texas, that there is almost complete population turnover in the course of a year. Parker found an average clutch of 4.05 (2 to 6) eggs in 57 females.

My own study of the brown-shouldered lizard was based chiefly on 1241 museum specimens. Little can be added to the thorough accounts of Tinkle. However, there is evidence of geographic variation in size of clutch, and much more striking evidence that time and duration of the breeding season is subject to geographic variation. A northern series from scattered localities in Washington, Oregon, Idaho, and northern Nevada compared with a southern series from various localities in San Bernardino and Riverside counties in southern California and from Baja California showed the following significant differences in size of clutch:

37 northern females averaged 2.73 ± .144 eggs (1 to 4)
73 southern females averaged 3.43 ± .13 eggs (1 to 6)

Table 5 indicates the span of the breeding season in different parts of the range. In the northern part gravid females are found only within the three month period May through July, but in southern California, gravid females have been found in seven months of the year and in Baja California they have been found in eight months.

Cuellar (1966:549) found that delayed fertilization may occur, with sperm remaining functional in the oviducts for as much as 81 days after copulation. Thirty adult females were captured early in the breeding season and kept isolated from males. In their first clutches they produced a total of 68 eggs of which 95 per cent were fertile, and in their second clutches there were 24 eggs of which 53 per cent were fertile. No eggs of the third clutches were fertile. Cuellar suggested that since regression of the male gonad begins by mid-July and egg-laying continues into August, many females may not be re-inseminated, but may depend on stored sperm for fertilization of late clutches.

Hoddenbach and Turner (1968:262) found that in southern Nevada the average clutch varies from year to year by as much as one egg, and that fertility is closely correlated with the crop of winter growing annual plants, which probably determine the population levels of the insects on which the lizards subsist.

Table 5. Ratios of Gravid Individuals in Adult Female *Uta stansburiana* Collected in Different Months and in Different Parts of the Geographic Range.

	Northwestern United States		Southwestern United States		Baja California	
	Number in sample	Percentage gravid	Number in sample	Percentage gravid	Number in sample	Percentage gravid
January	----	----	----	----	2	50
February	----	----	----	----	8	75
March	----	----	4	25	14	86
April	----	----	8	87	16	69
May	21	86	35	74	12	58
June	16	80	13	69	10	40
July	15	7	9	11	32	25
August	4	0	3	33	4	100
September	6	0	5	0	----	----
October	----	----	8	0	----	----
November	----	----	1	0	1	0
December	----	----	3	33	----	----

Agamidae

The agamids are a diverse family of Old World lizards, both north and south of the equator, noted for their parallelism with the New World iguanids in adaptive types. Many live in desert habitats, and cursorial types are common. Others are specialized in varying degrees for arboreal existence. Nearly all are oviparous but the highly arboreal *Cophotis ceylanica*, is viviparous, and the desert-living *Phrynocephalus* is also thought to be viviparous. In these two instances attainment of viviparity is probably a direct response to arboreal existence and to extremely xeric conditions, respectively. Insofar as records are available, most kinds of agamids that have been studied show evidence of a well-defined breeding season, even in the tropics; but, in the neighborhood of the equator, in *Draco* and possibly in *Goniocephalus* breeding occurs throughout the year.

Cogger (1967:40) wrote of Australian agamids that typically mating takes place in October or November, eggs are laid by the end of December, and young hatch in February or early March. He thought that a small proportion of females in a population produce two clutches in a season. He stated that scattered observations on the species of tropical northern Australia indicated that there might be breeding throughout the year.

Agama

These are small, terrestrial or scansorial lizards, many of them found in desert habitats. Breeding seasons indicated in several of the species cover periods of months, hence individual females probably produce several clutches of eggs. Breeding is concentrated in the spring months in Iran and North Africa; in South Africa the opposite time of year (the southern spring) is the chief breeding period.

Agama agama.—In tropical East Africa, Loveridge (1936:294) recorded gravid females March 23 to 29 and April 9 to 13, 1934. These contained 9, 10, 10 and 12 eggs.

At Gadomurtu, Kenya, 0° 01′ north latitude, at an elevation of 5800 feet, Marshall and Hook (1960:204) collected and studied a year-round sample of these lizards including 103 adult males, 109 adult females and 36 juveniles. Photoperiod as a seasonal factor was eliminated since the locality was so near the equator that difference in day-length was virtually nil. Nevertheless, the production of eggs occurred almost entirely within the period June through September and with a definite peak in July and early August. At that time of year eggs in three distinct phases of development were found in the same female: shelled eggs in the oviduct (usually numbering 10 to 12 per clutch), yolked eggs of intermediate size in the ovaries, and minute, colorless ovarian eggs which had not yet begun their growth. There was obvious correlation of the breeding cycle with changing food supply. In the dry season the lizards were much less in evidence, and those obtained often had relatively little food in their digestive tracts, with relatively large percentages of plant material. But during the season of the "long rains" in the summer months, the lizards were more active, usually had their digestive tracts crammed with insects, and rapidly accumulated fat bodies. In the period of the "short rains" in winter only one instance of egg production was noted; seemingly precipitation was usually inadequate to trigger a breeding cycle, or possibly breeding was inhibited by the relatively low nighttime temperatures at that time of year.

Another detailed study was made by Harris (1964:76, 82, 84) in Nigeria. At Ibadan he found that egg-laying begins about mid-February soon after the beginning of the rainy season, and that eggs can still be found occasionally as late as December; there is breeding through much of the year. However, at Kano and Zaria, farther from the coast, in a savanna type of vegetation, with a dry season lasting from November to April, the onset of the breeding season is delayed from six to eight weeks, with no breeding from December to March. Harris found that there are usually five or six eggs per clutch (3 to 8). About two months are required for incubation, and females were found to be sexually mature at an age of about 14 months.

At Accra, Ghana, Chapman and Chapman (1964:121) likewise found reproduction to be closely correlated with seasonal precipitation, with most breeding occurring during the main rainy periods or soon after them. The development of the gonads was thought to be related to the abundance of food, and ants were found to comprise a large part of the diet. At Suacoco, Liberia, Daniel (1960:94) found that the eggs, usually numbering from six to nine, are laid mainly in June and July, but with occasional production at other times of year. He concluded tentatively that sexual maturity was attained

in the second year at a snout-vent length of about 80 mm. Lizards of about 60 mm, twice the length of hatchlings, were thought to be one-year-olds.

Agama agilis.—In Iran, Anderson (1963:446) found that the short-tailed agama first appears in early March and is abundant by mid-April. All females taken between March 1 and July 18, 1958, were gravid. One that laid in captivity had other enlarged eggs in both ovaries. Obviously two or more clutches may be produced in a single season. Both newly hatched young and half-grown individuals have been seen in late October and early November. In West Pakistan, according to Minton (1966:94): "Indirect evidence such as the finding of large eggs in females and the development of bright colors by both sexes indicates that breeding begins in May and continues through early August." Minton observed small young from the first week of July through November.

Agama atricollis.—In tropical East Africa, Loveridge (1936:296, and 1942: 329) recorded gravid females on November 7, February 10 to 15, February 23, and May 7. In Angola, Manças (1963:228) reported that three females collected in September had eggs beginning to mature and in November one had large eggs.

Agama bibronii.—In Morocco, Bons (1964) found this species to have a breeding season lasting from March to August, with nine to 12 eggs per clutch having embryos already partly developed at the time of laying. In the western Atlas Mountains the breeding season is shorter, mid-June to mid-August, with two fairly distinct egg-laying periods.

Agama caucasica.—Khonyakina (1965:121) studied the natural history of this Caucasian species. He found that sexual maturity is attained late in the second year. Ovarian follicles begin to enlarge soon after emergence from hibernation. Mating occurs in May and June, and the six to 14 eggs, in a single clutch, are laid at the end of May or in June. Young appear in late summer. In West Pakistan, Minton (1966:94) noted evidence of breeding in early May and June ". . . with about a dozen eggs laid in June or July."

Agama cyanogaster.—Robertson, Chapman and Chapman (1964:310) studied this agama in the Rukwa Valley of southwestern Tanganyika in an equatorial climate. In a year-round sample of adult females there were gravid individuals in October (3 per cent), November (45 per cent), December (50 per cent), January (60 per cent), February (100 per cent), March (14 per cent), and none in April through September. Egg-laying and hatching occur mainly in the wetter part of the year. A similar pattern seemingly prevails in Nyasaland, where Loveridge (1953:178) noted that a female collected in July had only small ova, but on October 21, one had ova enlarged (6 mm) to about half of mature size and on November 29, December 2, and December 15 females with oviducal eggs were collected.

Agama hispida.—In Nyasaland, Loveridge (1953:179) noted that 12 females collected in January were all gravid, and had from 12 to 20 eggs. In South Africa, FitzSimons wrote that the eggs are laid in early summer, and about 14 constitute a typical clutch. In Angola, Manças (1963:230) mentioned a female containing four eggs in September, two containing eight and nine eggs in October and others containing eight, 10 and 12 eggs in November.

Agama inermis.—In Tunisia, Mosauer (1934:52) recorded a female with several large eggs on May 31.

Agama nupta.—In Iran, Anderson (1963:443) collected gravid female yellow-speckled agamas in March, August and October, indicating a remarkably long breeding season for a species occurring so far north in the Temperate Zone. In southern Baluchistan, Minton (1966:92) noted that breeding occurs in late February and March and that small young begin to appear in June and are found as late as November.

Agama persica.—In Iran, Anderson (1963:452) noted that a female in late August had eggs in her left ovary.

Agama planiceps.—Mertens (1955:57) recorded that a captive female of this South African species laid five eggs on February 5. He noted that the lizards were still hibernating in mid-September but were frequently observed in October.

Agama sanguinolenta.—This central Asian species is discussed in an undated book entitled "Reptile Life," an English translation (by Margot Schierl, published by Spring Books, London) of an original Czechoslovakian edition by Zdeñek Vogel. The female is stated to lay three batches of eight to 10 eggs per season, one batch in April, one at the end of May, and one in July.

Agama tuberculata.—M. Smith (1935:216) wrote of this western Himalayan species that it breeds from May to July and perhaps the early part of August. Females examined in May and June were carrying seven and nine eggs. The long breeding season observed indicates that probably two or more clutches are produced, by some females at least.

Amphibolurus

The bearded lizards of Australia comprise a large genus, with small, medium-sized, and large species. Seemingly their breeding is limited to the warmer half of the year. Waite (1929:101, 107) stated that the military dragon, *A. maculatus* of southern Australia, lays four or five eggs in February or March and that *A. pictus* of the central districts lays about eight eggs in late February or early March. Loveridge (1934:323, 324) recorded that a female of *A. diemensis* was gravid in early December, and that in September a female of *A. barbatus* had its body distended with 22 eggs. Worrell (1964:67) stated that in *A. barbatus* there are eight to 24 eggs in a clutch and that incubation lasts about three months. In northern New South Wales Bustard (1968:137) found that *A. barbatus* emerges from hibernation in September and is active until the end of May. Females are gravid in October and November (one contained six eggs). Young first appear at the end of December and are abundant by February.

Calotes

According to M. Smith (1935:180) this genus of the "bloodsuckers" has about 27 species in the Oriental region, East Indian Archipelago, and New

Guinea. They are strongly arboreal in habits, and oviparous. The available records indicate a breeding season beginning in spring and lasting for many weeks.

Calotes cristatellus.—In equatorial Bornean rain forest, Inger and Greenberg (1966:1017) collected eight gravid females, six of which each contained two eggs, while the remaining two each had only one.

Calotes emma.—In Thailand, Taylor (1963:900) noted that adults were ubiquitous in May but were scarce in the November rainy season. At the latter time the active population consisted chiefly of young of two distinct size- and age-groups: those recently hatched, 32 to 48 mm in snout-vent length, and a larger group, of 65 to 74 mm. The adult size is relatively large (typical snout-vent length 97 mm). Possibly two years are required to attain maturity, but it is probable that the size groups represent early and late broods of the same season, judging from the growth rate recorded in *C. versicolor.*

Calotes jerdoni.—M. Smith (1935:195) recorded copulation in a pair of these Indian lizards on August 25, and the finding of eggs in the Chin Hills on August 11.

Calotes mystaceus.—M. Smith (1935:199) recorded copulation of captives in Thailand on May 9, nesting on June 21, and hatching on August 20. There were seven eggs.

Calotes rouxi.—McCann (1940:53) wrote of this Indian agamid, "The breeding season commences during the hot weather, i.e. the middle of May, and reaches its height in June when the eggs are laid. The clutch numbers from 4 to 9, but 6 or 7 appears to be the general rule." He recorded clutches of 4, 6, 6, 6, 6, 6, and 9, average 6.1.

Calotes versicolor.—Asana (1931:1043) studied the natural history of the common Indian "blood-sucker" in the vicinity of Bombay. He found that breeding begins the first or second week of May and ends the first or second week of September. The testes undergo seasonal change in size that is much more marked than that in most other lizards and seemingly comparable to that in birds; at their minimum in mid-winter they are scarcely noticeable, but they enlarge rapidly in February and throughout the spring months. McCann (1940:51) wrote that at Andheri and Tulsi Lake, at the beginning of the breeding season, in April, females contained only ovarian eggs and had large fat bodies, but later in the season the fat bodies were exhausted. McCann (1940:51 and 1937:843) recorded clutches of 10, 11, 12, 14, 14, 15, 15, 17, 18, 21, 23, 23, and 23, average 16.6. Asana (1931:1045, 1046) incubated many eggs in the laboratory and found that they hatched in from 42 to 45 days. Individuals that he marked as hatchlings had attained sexual maturity when they were recaptured nine to 12 months later. In West Pakistan, Minton (1966:89) observed that there were females containing large eggs from early June through September, and he recorded that six clutches with six to 19 eggs were found between June 29 and October 22. At Varanasi, India, Pandha and Thapliyal (1967:122) found that egg-laying occurred from July 23 to August 23, and the clutch varied from one to 23.

Ceratophora

This genus, with only three species, is endemic to Ceylon and occurs in mountainous areas. The male has a prominent flexible nasal appendage. The habits are arboreal. M. Smith (1935:153) cited an instance of the finding of four newly laid eggs of *C. stoddarti* in January.

Cophotis

Of the two species in this genus one occurs in Ceylon, the other on Sumatra and Java. They are highly specialized for arboreal existence, having compressed bodies and prehensile tails. M. Smith (1935:151) stated of *C. ceylanica* that it is the only viviparous agamid except for *Phrynocephalus*. Specific details concerning reproduction seem to be lacking for both genera.

Draco

The flying lizards are small, delicate agamids in which the body has lateral winglike patagia that are collapsible and are supported by the last several pairs of ribs. When extended, the patagia support the lizard in long gliding flights from tree to tree. Also, the patagia function for display and are brightly colored in gaudy patterns that differ between species and sometimes differ between the male and female of the same species. Although almost exclusively arboreal, these lizards come to the ground to lay their eggs, and the female digs a burrow for this purpose. The genus has one species in southern India and many in the Malayan region, the Philippine Islands, and the East Indian Archipelago.

Draco dussumieri.—McCann (1940:46) wrote of this Indian species that the breeding season is undoubtedly during the monsoon rains. In each of three gravid females he found four eggs. Taylor (1963:820) noted that four eggs are the usual clutch also in *D. fimbriatus, taeniopterus, volans, formosus,* and *maculatus.*

Draco melanopogon.—Large series of these lizards were collected by Inger and Greenberg (1966:1012) in their study of reproductive cycles in equatorial rain forest lizards at Nanga Tekalit, Borneo. Breeding males and gravid females were collected in every month of the year. In most months, when substantial samples of females were obtained, between 40 and 85 per cent contained oviducal eggs, with no evident seasonal trend. Six females each contained only one oviducal egg and 76 had two (one in each oviduct). Ovarian eggs of 2.0 mm or less usually were white and those of 2.5 mm diameter or larger were yellow, indicating that yolk-deposition and growth were in progress. Females that had the largest oviducal eggs (larger than 16 mm in length) usually also had relatively large and yellow ovarian eggs, whereas in the females with smaller, recently ovulated eggs, the ovarian eggs were minute and white. Seemingly when eggs, one on each side, are ovulated and enter the oviducts there is a temporary inhibition of growth in the remaining ovarian eggs while those in the oviducts continue to grow. When the oviducal eggs reach a length of 16 to 17 mm, one egg in each ovary resumes its growth and accumulates yellow yolk material in preparation for the next ovulation.

Draco obscurus.—This species also included in the study by Inger and Greenberg (1966:1012) in Borneo was found in relatively small numbers. Only 15 adult females were captured; nine of them were gravid, and these were distributed over six months of the year. Each of five gravid females contained four eggs, two each contained three eggs and one contained one.

Draco quinquefasciatus.—A total of 266 were examined by Inger and Greenberg in Borneo. All adult males were reproductively active, regardless of time of year. Gravid females were collected in all months, and showed no distinct seasonal trend, but usually made up between 30 and 50 per cent of each monthly sample of adult females. Thirty-eight gravid females each contained three eggs, 18 had two eggs, four had four eggs, and two had one. As in *D. melanopogon,* there seemed to be a pause in development of ovarian eggs after an ovulation, and the gravid females with recently ovulated eggs in their oviducts had only small white eggs in their ovaries.

Goniocephalus

These highly arboreal agamids occur in southeastern Asia and the Indo-Australian Archipelago.

Goniocephalus grandis.—In equatorial rain forest at Nanga Tekalit, Borneo, Inger and Greenberg (1966:1017) obtained 27 gravid females; 13 each had three eggs, 12 each had four, and there was one each with one and five eggs. The gravid females were distributed over 11 months of the year, suggesting that breeding continues uninterruptedly.

Goniocephalus liogaster.—This was another of the species studied by Inger and Greenberg in Borneo. Of 22 gravid females, 12 each had three eggs, eight each had four and two had one. As in *G. grandis,* gravid females were obtained in 11 months of the year, suggesting that breeding is continuous in this species as it was demonstrated to be for several others that were represented by larger samples.

Leiolepis

This Oriental genus includes medium-large, terrestrial and cursorial lizards, which live in burrows in open sandy situations. They are of flattened body form. *L. belliana* is widely distributed in southeastern Asia. M. Smith (1935: 241) cited a statement by Annandale that ". . . it is monogamous, a single pair inhabiting a burrow which is shared by several young ones, probably hatched in March or April. . . . They lay large oval shaped eggs."

Moloch

This is a monotypic genus including only the thorny devil, a small, squat, myrmecophagous, spiny-bodied agamid which occurs throughout much of the arid region of the Australian interior. Cogger (1967:40) stated that in *M. horridus* mating generally takes place in October or November, the eggs, often six to eight, are laid by early January, and the young hatch in late February or early March.

Otocryptis

This genus has only two species of small to medium-sized, forest lizards in India and Ceylon. M. Smith (1935:147) cited a statement by Deraniyagala that in *O. wiegmanni* there is no definite breeding season and that there are three or four eggs in a clutch.

Phrynocephalus

The toad-headed lizards are a group of more than 40 species in the deserts of central Asia. M. Smith (1935:228) wrote of the genus: "It is also said to be viviparous. Embryos, usually two in number, in a well-advanced stage of development, can be found in the females, but always in conjunction with a large yolk-sac. How far development proceeds before the young are born is not known." In West Pakistan, Minton (1966:97) noted that females of *P. luteoguttatus* contained two to four large eggs in May and that young were abundant in late August.

Sitana

These small lizards of India and Ceylon are terrestrial and sometimes bipedal, usually living in open situations. M. Smith (1935:146) recorded courtship by the fan-throated lizard, *S. ponticeriana*, in the latter half of August and finding of young on October 14. He stated that there are six to eight eggs per clutch. McCann (1940:48) mentioned a female from near Belgaum, India, that laid 11 eggs on June 7, 1938, after two days in captivity. Chopra (1964:190) reported that in 1963 a captive female from near Poona, kept with two males, laid successive clutches of eggs on August 29, September 17, and October 10. There were 11, 13 and 14 eggs. Copulation was seen on August 31—two days after the first laying—and vigorous courtship was noticed after the second laying, in the third and fourth week of September.

Uromastix

The spiny-tailed lizards are large, heavy-bodied, herbivorous, desert-living agamids which live in burrows, in southwestern Asia and northern Africa. Mosauer (1934:53) stated that a female *U. acanthinurus* brought alive from Tunisia to Vienna laid eight eggs on June 25. In West Pakistan Minton (1966:91) found that the breeding season of *U. hardwicki* is in March and early April; eight to 14 eggs are laid from April to early June, and young begin to appear in late June.

Chamaeleontidae

The chameleons are mostly specialized for arboreal existence. They are limited to the Old World and chiefly to the African and Madagascan tropics. The genera *Brookesia* and *Rhampholeon* are oviparous; *Microsaura* is viviparous and the large genus *Chamaeleo* has species in both categories. A notable aspect of reproduction in

chameleons is their retention of viable sperm in the oviduct long after mating, and the occasional fertilization of a new batch of ova before the embryos of an earlier lot have reached full term.

Brookesia

The stump-tailed chameleons are oviparous lizards of partly terrestrial and partly arboreal habits, in Africa and Madagascar. Loveridge (1936:335; 1942:371; 1951:181; 1953:193-194) recorded field notes concerning fecund females of the East African species. One of *B. brachyura* contained six eggs. One of *B. platyceps* contained ovarian eggs in late June or early July; another was ovipositing on February 17. One of *B. spectrum* was gravid on January 18 and another on February 20. There were three eggs in one clutch. One of *B. kersteni* contained three eggs 3½ mm in diameter on April 24 and on June 12 another contained six eggs about 2 mm in diameter. The holotype of *B. ionidesi,* collected in January, contained fully developed eggs, and others contained large eggs on February 20, 22, and 25 and March 1 (two) and 8.

Chamaeleo

These chameleons occur chiefly in tropical Africa, but also in Ceylon, Arabia, along the southern coast of the Mediterranean and in southern Spain. Some are oviparous and others are viviparous. Also there are two well-defined categories of tropical species as regards extent of breeding season. In one group of species breeding occurs throughout much of the year, whereas the other group has a short breeding period. Schmidt and Inger (1957:95) pointed out that the viviparous species in general occur in cooler climates (farther south or at higher altitudes). Also, they pointed out the advantages conferred by viviparity in these specialized arboreal lizards.

Chamaeleo basiliscus.—Shaw (1960:182) observed several of these chameleons received from northern Nigeria on October 10, 1957. A female was digging a burrow on December 4, and on December 7, 23 eggs had been laid at the end of a 20-inch burrow. Hatching occurred 169 to 183 days later (average 172.8 days).

Chamaeleo bitaeniatus.—Bustard (1966:14) studied the reproduction of the side-striped chameleon, a large species of the East African highlands, and noted births in the months of April, May, July, September, October, and November. Loveridge (1936:333) found that in one group of females collected from December 12 to January 17, most contained from nine to 22 eggs. On December 28, 10 of 30 females in another group were gravid, containing eggs in various stages of development, with the following numbers: 5, 6, 6, 7, 7, 8, 9, 9, and 10. Bustard concluded that possibly these lizards breed throughout the year and he observed that females are noticeably gravid for as much as three months prior to parturition. In five females examined by Bustard fetuses numbered 10, 14, 17, 19, and 21. One gravid female contained 18 fetuses that were nearly full-term and three embryos that were relatively minute and were thought to represent a more recent ovulation. Similarly, another female contained 15 large and two minute embryos. After extensive

field work on chameleons in East Africa, Philip W. Ogilvie stated *(in litt.)* "The chameleons around Lake Victoria seem to have no particular breeding season, and one can find, in the same sample of animals, females with all stages of development *in utero*, of *C. bitaeniatus, C. hohnelii* and *C. jacksoni* . . . I found ovaries with undeveloped ova, completely developed ova, and some term embryos."

Chamaeleo chamaeleon.—The common chameleon is a species of the southern Mediterranean region. Bons and Bons (1960:323) found that eggs kept in the laboratory required 250 to 260 days for incubation. Mating occurs in August or sometimes in September, and eggs are laid about mid-October. Thus the annual breeding cycle differs greatly from those of lizards of other families that occur in the same region.

Chamaeleo dilepis.—Loveridge (1936:330; 1942:363; 1953:184) recorded gravid females of the flap-necked chameleon at various localities in tropical East Africa in March, April, May, July, and November. He recorded clutches of 23, 26, 36 and 36 eggs. In a series of 20 adult females collected September 24 to 30 none had enlarged ova. In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman, and Chapman (1962:423) noted that one caught in February had 49 enlarged follicles in the left ovary and 46 in the right, averaging 5.5 mm—a remarkably large complement for any lizard, but perhaps not all of them would have matured. In the tropical portion of the range seemingly there is a long breeding season, but with interruptions during the less favorable parts of the year. FitzSimons (1943:154) stated that in South Africa 40 to 50 eggs are laid in late summer and incubation lasts about three months. Manças (1963:232) reported that in Angola females did not have enlarged ova in August, September, October, or November.

Chamaeleo gracilis.—Loveridge (1936:330) wrote that in 30 females collected in mid-January at the base of Mt. Elgon, Uganda, all ova were minute.

Chamaeleo hohnelii.—Bustard (1965b:403) kept a group of these montane East African chameleons and recorded number of young in six litters. There were 8, 8, 9, 11, 11, and 11 young, average 9.7. He recorded births of litters on August 20, September 19 and October 10.

Chamaeleo melleri.—Loveridge (1953:188) mentioned a clutch of 70 eggs laid by one of these giant one-horned chameleons from Zomba, East Africa, but quoted an informant to the effect that the average number is near 50. Philip W. Ogilvie *(in litt.)* informed me that in Tanganyika the young of this species all hatch within a 30-day period, mainly June.

Chamaeleo rudis.—Rand (1963:20) stated that all of the six females in the type series of *C. r. sternfeldi* at Mt. Meru, Tanganyika, contained eggs in August 1957.

Chamaeleo senegalensis.—Loveridge (1929:84; 1936:329; 1942:362) recorded gravid females of this tropical East African species on January 8, March 13, and July 12, indicating a lengthy breeding season, or perhaps breeding throughout the year. Three of the females contained 7, 14, and 60 eggs.

Chamaeleo zeylanicus.—M. Smith (1935:252) observed this Asiatic species in captivity and recorded mating on October 5 and 6, nest-making on Novem-

ber 9, and egg-laying on November 11. In West Pakistan, Minton (1966:99) observed copulation in captive chameleons on October 10 and 11, and reported that four females laid clutches of 10 to 18 eggs between November 25 and December 12.

Microsaura

The several species of small, viviparous chameleons of this genus are endemic to southern Africa.

Microsaura pumila.—Atsatt (1953:59) observed the reproduction of this species in captivity. A female captured on January 5, 1940, and caged with other females, produced a litter of young on February 23. On April 26 and May 3, after an injection of pituitrin, she aborted embryos, indicating retention of viable sperm from a mating prior to capture. On July 16 to 19 she aborted eight more embryos. On November 12 she aborted 13 eggs, and again on March 24, 1942, she aborted a clutch of 13 eggs. Busack and Busack (1967:231) obtained a gravid female from near Capetown and she produced successive litters on November 3 and 14, 1959, and February 20, 1960. Although caution must be exercised in extrapolating from these observations to animals living under natural conditions, it is probable that litters are produced from closely consecutive, or even overlapping, pregnancies, with no restricted breeding season. Bustard (1955:6) wrote that a captive female gave birth to 11 young on April 22. She had been received earlier the same month. FitzSimons (1943:164) stated that in South Africa a litter of about eight to ten young is born in midsummer.

Microsaura ventralis.—Bustard (1963b:704) recorded a mating of captive individuals on July 23, 1953. The female died after three months, and contained 13 well developed embryos. FitzSimons (1943:171) stated that a female in South Africa dissected in November contained 20 embryos in an early stage of development.

Rhampholeon

These small, oviparous, arboreal chameleons occur chiefly in the African tropics, but one species, *R. marshalli*, lives in South Africa, where FitzSimons (1943:173) reported gravid females in December. There were 12 to 18 eggs.

Xantusiidae

This family of small, geckolike, viviparous, terrestrial lizards has only a few genera and species, with a discontinuous distribution in the West Indies, Central America, and the southwestern United States.

Klauberina

This is a monotypic genus of insular and relatively large xantusiids confined to the Channel Islands off the coast of southern California. Brattstrom

(1951:143) recorded females of *K. riversiana* from San Clemente Island containing 4, 5 and 6 eggs, and he recorded females from San Nicolas Island with 6, 7, 8, and 9. Amrein and Amrein (1951:180) collected females on San Nicolas in early September which contained three and four nearly full term embryos.

Lepidophyma

This genus is confined to a limited area, mainly of humid tropical lowland in Central America. Stuart (1948:55) wrote that a female of *L. flavimaculatum* from Alta Verapaz, Guatemala, contained six eggs on March 29, 1940.

Xantusia

This genus has species in arid regions of the southwestern United States.

Xantusia henshawi.—Brattstrom (1951:143) stated that there are usually two young.

Xantusia vigilis.—Miller (1951:117) described the breeding cycle of this common desert lizard. Spermatogenesis is in fall and spermiogenesis is in spring. Copulation usually occurs in the last week of May and the first week of June. Gestation lasts approximately 90 days. Of 78 gravid females, 60 had two embryos, 17 had one, and one had three. Corpora lutea are prominent throughout pregnancy. Males attain sexual maturity late in their second year, but in females breeding is delayed until the third year. Miller (1954:38) found that both the prevalence and the timing of breeding were greatly affected by differences in the weather from year to year. In 1951, an unusually dry year, many females either did not produce eggs, or resorbed them early in pregnancy. Of 32 adult females examined only two were gravid. In 1940, a relatively dry year, ovulations occurred mostly in the first ten days of June. In 1952, a relatively wet year, ovulation did not occur until the last week of June or the first week of July.

Bartholomew (1953:45-50) performed a series of experiments to test the interaction of light and temperature in controlling the gonadal cycle of the night lizard. Males proved to be much more responsive than females to the experimental treatment. Groups of lizards were kept for periods of weeks in late fall and winter in artificial light for 16 hours per day. Different groups were kept at temperatures of 8°, 20° and 32°. At the higher temperatures males showed a much accelerated rate of gonadal development, comparable with that of the more responsive kinds of birds. The females showed only limited response in ovarian development. The photoperiodic response of the female was insufficient to take the ovaries beyond the first stages of reproductive development, and was virtually independent of temperature.

Scincidae

The skinks are a large family of rather primitive lizards of world-wide distribution in temperate and tropical regions. Most species and genera are tropical. Presumably viviparity has devel-

oped many times independently in the family; according to Greer (1968:171) 95 viviparous species are known, and 152 oviparous species. Most genera are either exclusively oviparous or exclusively viviparous, but the genera *Eumeces, Leptosiaphos, Mabuya,* and *Sphenomorphus* all include species of both types. I have followed Mittleman's (1952) systematic arrangement of the lygosomine skinks, resulting in a partitioning of the large genus *Lygosoma (sensu latu)* into many smaller generic units—even though this arrangement has not been universally accepted by herpetologists.

Ablepharus

These oviparous skinks occur both in the tropics and the Temperate Zone in the Old World. The meager information available indicates that in temperate regions they follow the usual pattern of breeding in spring (at opposite times of year in the northern and southern hemispheres), and that in the tropics the annual breeding cycle is timed so that the young appear in the rainy season.

Ablepharus boutonii.—On a voyage in the Central Pacific in September to October, and December, 1966, John H. Fitch (pers. comm.) collected 102 of these skinks on seven small islands. He found gravid females only on Howland Island in September and Baker Island in October. In December several hatchlings were observed on Enderbury Island. McGregor (1904:117) recorded finding eggs on Maui, Hawaiian Islands, on December 19. Hatching occurred on January 30.

Ablepharus kitaibelii.—In Romania, Fuhn and Vancea (1961:186) reported that courtship and mating of this dwarf skink takes place in mid-April, laying in early June, and hatching in August.

Ablepharus wahlbergii.—FitzSimons (1943:238) stated that in South Africa the eggs of the savanna snake-eyed skink are laid in spring or early summer. In tropical East Africa, Loveridge (1936:328; 1953:216) observed, "Clearly the two eggs laid by this species hatch during the rains (mid-November to mid-March in normal years)" and he mentioned hatchlings found November 30 and gravid females on February 17 and 28. These females had 4, 5, and 6 eggs.

Acontias

These are small, highly fossorial, limbless, short-tailed viviparous skinks of South Africa and East Africa. FitzSimons (1943:244) reported that in *A. meleagris* of Cape Province, South Africa, the three or four young are born in late summer or early autumn.

Carlia

These small oviparous lygosomine skinks of Australia, New Guinea, and the Moluccas are of lacertiform habitus with well developed limbs.

Carlia fusca.—In this tropical skink of northern Australia, there is a definite breeding season, from October through February. Wilhoft and Reiter (1965: 385, 386) made a study of the breeding cycle at 16° south. Field work was carried on from October through March. The monthly ratio of females with oviducal eggs to other adult females for part of the year was as follows: October, 2 of 10; November, 7 of 18; December, 11 of 18; January, 6 of 14; February, 7 of 13; March, none of 11. All gravid females contained two eggs, one in each oviduct. During March the gonads and accessory sex structures of both sexes regressed in size, but by October both sexes were again reproductively active. Field work was discontinued from April through September.

Carlia rhomboidalis.—In northern Australia Wilhoft (1963) found that the males of this tropical skink were capable of reproductive activity throughout the year. In females productivity was relatively low in the colder half of the year, as shown by the following ratios of gravid individuals in monthly samples: 7 of 46 in January, 8 of 42 in February, 7 of 46 in March (no sample in April), 1 of 5 in May, 1 of 5 in June, none in July or August, 2 of 22 in September, 4 of 66 in October, 4 of 33 in November, and 8 of 42 in December. Each gravid female had two eggs.

Chalcides

Members of this genus are desert skinks of North Africa and southwestern Asia. They are viviparous and seem to have a relatively short spring breeding season.

Chalcides ocellatus.—In Tunisia, Mosauer (1934:54) noted, "In the period from April 30 to May 11, 1928, almost all the females of the large number examined contained eggs with developing embryos . . . from three to eight but almost all the females contained six to seven eggs." He found the embryos to be further advanced in the larger and older females. Mendietta (1962:159) likewise found a brief reproductive period with pregnancies beginning in May and terminating some 50 days later, at the end of July. The volume of the fat bodies was found to be in inverse ratio to the volume and activity of the gonads. The skinks were found to attain sexual activity in the second year of life. Kehl and Combescot (1955:58) described a simple chorio-allantoic placentation in the ocellated skink.

Chalcides tridactylus.—Mosauer (1934:55) noted females of the three-toed desert skink with ovarian eggs on April 19; four days later he found one that had fertilized eggs in its oviducts. Kehl and Combescot mentioned this species as having a complex chorio-allantoic placentation, more advanced than that found in *C. ocellatus.*

Egernia

The Australian spiny-tailed skinks are robust, coarse-scaled lizards generally found in arid, rocky habitats. They are viviparous. Hickman (1960: 111) observed the annual cycle of *E. whitii* in the vicinity of Hobart, Tasmania. He found that mating occurs in spring (October) and most births occur in February. There are from one to five young per litter. Seemingly at least four

years are required to attain fully adult size of 80 mm snout-vent length. *E. cunninghami* is a montane Australian species; Worrell (1964:39) stated that it has litters of about three young.

Emoia

These small, smooth-scaled skinks having relatively short bodies and well developed limbs, are widely distributed on islands of the Pacific, even in Polynesia.

Emoia atrocostata.—Alcala and Brown (1967:596-604) studied the ecology of this tropical skink on Negros Island in the Philippines. It was concluded that breeding occurs throughout the year, because young of hatchling size or not much larger were observed in every month, but no definite seasonal peaks were discernible. The usual clutch was two eggs. Incubation averaged 60 days in the laboratory. Maturity was attained within nine or ten months from the time of hatching. The population consisted of about 71 per cent first-year individuals. The maximum age attained in a large sample of marked individuals was between three and four years.

Greer (1968:418) noted that in most species of *Emoia* including *atrocostata, callisticta, cyanogaster, cyanura, loveridgei, mivarti, nativitatis, pallidiceps, physicae, ruficauda, sorex* and *submetallica,* the clutch of eggs is normally two, but that several exceptionally large species produce more eggs per clutch.

Emoia cyanura.—Baker (1947:245) made a year-round study of the reproduction of this species in tropical rain forest, at 15° 15′ south latitude on Espiritu Santo in the New Hebrides. In this locality there was no dry season, mean temperature varied only 2° C between the coolest and hottest month, and day-length differed only one hour and 48 minutes from summer to winter. Under these conditions breeding occurred throughout the year but with a definite peak in "summer"—November and December—and relatively few eggs were produced at the opposite time of year, in May and June. Testis-weight in males varied seasonally, tending to parallel egg production in females, with a summer maximum and winter minimum. In the Central South Pacific, John H. Fitch (pers. comm.) found no gravid females among many of these lizards seen on Hull Island in October. He reported a female in a nest (probably communal) with 11 eggs on Fanning Island, March 17, 1964.

Emoia nigra.—In this large species (78 to 118 mm snout-vent length), Greer (1968:418) found two to four eggs, average 2.4, in 11 females.

Emoia samoense.—Greer (1968:418) found five eggs in a female of 96 mm snout-vent.

Emoia wernеri.—In a study by Baker (1947:245) in the New Hebrides, the seasonal cycle of this species was found to parallel closely that of *E. cyanura* as discussed above.

Eumeces

This is a large genus of skinks, confined to the Northern Hemisphere but found in both the New World and the Old World, with the majority of species

occurring in the Temperate Zone but some occurring in the tropics. The few viviparous species are the exceptions; most are oviparous, and these are notable in that the female ordinarily remains in the nest with the eggs throughout their incubation. Even after hatching, the family group may remain together for a short time. Hence the female produces but one brood per year. Breeding is normally in spring, but occurs in fall in the Floridan *E. egregius*.

Eumeces brevilineatus.—This is a medium-small species of southwestern Texas and adjacent México. Werler (1951:40) wrote that at the San Antonio Zoo eggs were laid in April and May. Sabath and Worthington (1959:31) recorded a clutch of eight eggs laid on June 3, 1958. On May 28 a female was found by them to contain eight eggs.

Eumeces callicephalus.—Campbell and Simmons (1961:212) reported finding an incubating female in Jalisco, México, on August 14, 1960. The female was coiled around the three eggs, in a depression. One of the eggs hatched on September 1, and the hatchling was eaten by the female. The two remaining eggs hatched on September 5. Zweifel (1962:64) recorded that a female from Nayarit, México, laid six eggs on July 18 and hatching occurred on July 26, after a remarkably short incubation period.

Eumeces copei.—Smith and Laufe (1945:338) recorded a juvenile of 32 mm snout-vent collected southeast of México City on July 3, 1942. Presumably this individual was born in early June or May. An early breeding season is indicated.

Eumeces dicei.—Axtell (1960:23) established the viviparity of this montane species of northeastern México, and recorded four gravid females, each having three large embryos on July 6 and 7.

Eumeces egregius.—Mount (1963) studied the natural history of the red-tailed skink in Florida and southern Georgia. He found that the species is notably different from other members of its genus in that it mates in autumn—September or October. Inseminated females undergo a period of postmating quiescence when they remain underground, almost totally inactive, for many weeks. In 14 captive females that had mated, nest burrows were dug and eggs were laid between April 3 and June 15, 1960. Incubation required 31 to 51 days. The female remains with her eggs throughout their incubation. Hamilton and Pollack (1958:25) uncovered an incubating female at a depth of four inches on June 15, 1950. The same authors noted that enlargement of ovarian eggs begins in late summer and continues through the autumn, winter, and early spring. Although copulation occurs typically in early autumn, it may be delayed until spring; for example Babbit (1951:79), observed copulation at Key West on March 13, 1946. Mount (1963:375) found an average of 4.8 (2 to 9) eggs in 13 clutches.

Eumeces fasciatus.—The natural history of the common five-lined skink was studied by me (Fitch, 1954) at The University of Kansas Natural History Reservation near the northwestern limit of the range of the species. The skinks normally emerge from hibernation in late March. Seemingly hibernation and emergence trigger the breeding cycle, since individuals that have begun to hibernate can be brought into breeding condition in midwinter by keeping

them at high temperatures for a little more than two weeks (Fitch, 1954:46). Normally breeding activity reaches its peak in the second week of May, and is marked by the assumption of pugnacious behavior and of bright orange-red suffusion of the head in males. A female may mate with several males over a period of days, and within a week or two the resultant hormonal changes cause her to become more secretive, remaining in hiding and excavating a nest burrow in decaying wood or damp soil. In late May or June the eggs are deposited in the nest burrow, which is usually not more than three inches deep and typically is beneath a flat rock in a situation exposed to sunshine for at least part of the day. During incubation the female emerges only occasionally for short forays, and is usually in the nest cavity with her body looped around the eggs, which are kept in a compact cluster. The female may defend the eggs against small predators, and may moisten them by voiding the contents of her bladder on the floor of the nest cavity. By further burrowing activity she may displace the nest cavity upward or downward from its original position, thus regulating in some degree the amount of moisture. Two or more females often have their nests near together, in connecting but distinct excavations. Being sluggish and little inclined to forage during incubation, the female becomes somewhat emaciated, and she may eat some of her own eggs. Much of the female's season of activity is used up in preparing a burrow for the eggs and in tending them after they are laid; there is no possibility of a second clutch the same season. Hatching occurs from the last week of June until August. For 64 clutches the mean was 9.16 eggs per clutch, ranging from four to 15. In typical populations approximately half of the egg-bearing females are two-year-olds, and these newly matured individuals lay fewer eggs, on the average than do old adults. For 24 females 65 to 70 mm in snout-vent length, the clutch averaged 8.2 eggs, whereas for 40 females of 71 to 78 mm the clutch averaged 9.7.

Eumeces inexpectatus.—In southern Florida Duellman and Schwartz (1958: 290) noted copulation on June 24, 1953. On the same day they found a female coiled about a clutch of 11 eggs under a log, and hatchlings were collected in June. In Mississippi Smith and List (1955:120) recorded a clutch of 11 eggs, in a natural nest that hatched on August 14. Obviously the breeding season is much less restricted than in *E. fasciatus.*

Eumeces laticeps.—Goin and Goin (1951:30) observed a small colony of these skinks in their yard at Gainesville, Florida, over a period of years. They found that even in the mild Florida climate hibernation lasts from the third week of September (adults) or the second week of October (young) until late March or early April. In this colony hatchlings appeared in late June or early July. In Georgia Martof (1956:111) found a clutch of 13 eggs on June 13; a captive female that he kept laid a clutch of 16 eggs on June 11. Another female was found by Martof brooding her clutch of 15 eggs on September 18, 1955. The remarkably late date caused the author to speculate that some eggs may fail to hatch the season they are laid, and that they may not be able to withstand the winter. However, experiments have shown that embryos of *Eumeces fasciatus* are not harmed by temperatures near freezing (A. V. Fitch, 1964:184). The female involved was a relatively small one and may have matured too late to produce her clutch at the usual time. Carr (1940:76) recorded copulation in confined greater five-lined skinks on May 2, and eggs were laid on June 3. In general the few recorded clutches of *E. laticeps*

markedly exceed in number of eggs those of *E. fasciatus*. The normal number of eggs per clutch cannot be stated with precision because of the possibility that some of the recorded clutches pertain to individuals of *fasciatus* or *inexpectatus* and others may be composites.

Eumeces latiscutatus.—Fukada (1965:74) noted the paucity of literature concerning this common Oriental five-lined skink, and cited a record of a copulating pair on Kyushu in the early summer of 1955, and the finding of seven oviducal eggs in another female.

Eumeces lynxe.—This montane Mexican species is remarkable in being viviparous. Tanner (1958:62) recorded a female from Durango that had two fully developed embryos. Werler (1951:40) wrote that of two females captured at Las Vigas, Veracruz on January 16, 1950, one gave birth to five young on March 12, and the other had three young on March 17. The same author (1949a:67) wrote that a female from five miles south of Tezuitlan, Pueblo, November 17, 1948, produced young on January 15, 1949.

Eumeces multivirgatus.—Gehlbach and Collette (1959:142) wrote that an adult male taken in Nebraska on June 26, 1957, had enlarged testes and red head indicative of breeding condition. On the same date two adult females had ovarian follicles only slightly enlarged—1.8 mm or less in diameter. A late breeding season is indicated. In the Zuni Mountains of northwestern New Mexico, Gehlbach (1965:296) found two incubating females in nest burrows with their clutches of three and five eggs, on June 28, 1954, and August 7, 1957. Another female was found with a brood of four hatchlings on August 17.

Eumeces obsoletus.—The Great Plains skink breeds in May in northeastern Kansas. Nest burrows, usually under flat rocks, can be found with gravid females in late May and early June, or with clutches accompanied by the female in late June, July or early August. However, many adult females captured in the same months are not in nest burrows and are neither gravid nor parturient. Seemingly in any one year a substantial proportion of them fail to breed. Those that do breed remain with the eggs throughout their incubation. Eggs hatch in July (usually the latter half) or in August. The smallest fecund female examined was 105 mm snout-vent, but many others of approximately this size were not carrying eggs. Judging from the growth rates of marked young of various sizes, females do not mature until the third year at the earliest, and probably most often the fourth year, after 13 or 19 months of active life. (Hibernation extends from mid-October to mid-April.) Rate of growth differs greatly among individuals. Males are sexually mature in their second or third years. In 12 egg-bearing females the number of eggs varied from seven to 17 and averaged 11.0. A recently completed intensive three-year study of a population of Great Plains skinks in northeastern Kansas, by Russell J. Hall, bears out and extends these findings.

Eumeces ochoterenae.—Near Chilpancingo, Guerrero, México, Davis and Dixon (1961:50) found adult females in June that appeared to have produced eggs recently. A hatchling was taken on June 18.

Eumeces septentrionalis.—In southeastern Minnesota, Breckenridge (1943: 591) studied a colony of prairie skinks and found that there are five to 13 eggs

per clutch, laid from the end of May to mid-July. Young attain maturity at the end of the second year. Clarke (1955:163) mentioned clutches of 6, 7, 9, and 10 eggs laid by females in Osage County, Kansas, June 23 to 27. Gehlbach and Collette (1959:142) mentioned an exceptionally large (84½ mm snout-vent) Nebraska female that contained 18 eggs and a smaller female that contained 11 on June 8, 1956. On this date males had red heads and still appeared to be in breeding condition. In northeastern Kansas the prairie skink breeds several weeks later than the five-lined skink in the same localities. Sabath and Worthington (1959:31) mentioned a Texan female only 60 mm in snout-vent length which laid nine eggs on May 26 and 27.

Eumeces skiltonianus.—The breeding of this western species is known chiefly from the observations of Tanner (1943, 1957) in Utah. He stated that mating occurs in May or early June. Females with large ovarian eggs were found through June to July 2. One female laid eggs on July 9. Recent hatchlings were found in nests on August 3, August 3, August 21, and August 23. In 20 clutches or broods mentioned by Tanner the mean was 4.25 eggs, with four in 11, five in six, and with six, three and two eggs each in one. Some indication of geographic variation in size of clutch is provided by the statement of Stebbins (1954:283) that eight females from California contained seven to 10 ova with an average between eight and nine; but, as pointed out by Tanner, some of these eggs were small and perhaps would not have developed.

Eumeces tetragrammus.—Werler (1951:41) recorded that a female from Laredo, Texas, laid 12 eggs on April 27, 1950, and another laid a clutch of five eggs on May 4.

Eumecia

These viviparous lygosomine skinks of Nyasaland, East Africa, are of vermiform habitus, with limbs much reduced. At Kaimosi, Loveridge (1936:324) found four to eight embryos in four females of *E. anchietae* collected in mid-February.

Hemiergis

This genus includes viviparous lygosomine Australian skinks so specialized for fossorial existence that the body is vermiform, limbs are greatly reduced and ear opening is minute. In *H. peronii* of western Australia, Smyth and Smith (1968:575) found that ovulation occurs in October (spring) when male testes are at their smallest and males lack motile sperm. It is inferred that copulation occurs only in autumn and that fertilization is accomplished by sperm stored in the females' oviducts during winter. The two to four young are born in late February or early March.

Isopachys

The one species, *I. gyldenstolpei*, is endemic to Thailand and is limbless, fossorial, and little known. Taylor (1963:1064) obtained a female which contained five embryos, demonstrating viviparity.

Lamprophotis

This genus includes lygosomine skinks of Australia, New Caledonia, and the New Hebrides and Loyalty Islands. They have well developed limbs, and are oviparous. Worrell (1964:46) wrote of the common Australian *L. guichenoti* that it lays two or three eggs, often in community laying areas, beneath stones or among grass roots.

Leiolopisma

Species of this lygosomine genus occur in Australia, New Zealand, New Caledonia and West Africa; they are of lacertiform habitus with well developed limbs, and some or all are viviparous.

Leiolopisma aeneum.—Barwick (1959:344) obtained limited data for this New Zealand skink, along with more extensive information for the commoner *L. zelandica.* The two are alike in having a long hibernation period, from some time in April through August, and a spring breeding season, which was found to be some two weeks earlier in *L. aeneum.* Several females of the latter had ovulated by September 22 when a small series was collected. *L. aeneum* is viviparous. Of 13 fecund females, 11 each had two eggs or embryos, and the other two each had three.

Leiolopisma zelandica.—This common New Zealand skink was studied year-round by Barwick (1959) at Wellington. He found that ovulation occurs in early spring (October) and that females ovulate for the first time when they are 21 months old and have recently emerged from the second hibernation. After an ovarian resting period, new ova begin to enlarge in March, are four to five mm in diameter by late June (the middle of the hibernation period), and are as much as 6.5 mm in diameter by the time of ovulation in October. Gestation lasts about three months. The lizards are viviparous, with well-developed placentation. Births are concentrated in January. There is only one litter per female per year. In 33 females there were, on the average, 5.02 eggs or embryos; two had two, 12 had four, six had five, nine had six, two had seven and two had eight. In the male, Barwick found that testes were smallest during hibernation—mid-April through August—increased in mass in spring—September through December—and had sperm present in epididymes through January, February, and March.

Leptosiaphos

These East African ground skinks resemble *Lygosoma* but have better developed limbs. Seemingly there are both oviparous and viviparous species. In the Mubuku Valley, Loveridge (1942:351 and 354) found five females of *L. graueri* in various stages of pregnancy in early January. In the same period one female of *L. kilimensis* contained only two small ova whereas two others contained oviducal eggs, and three clutches of eggs that were hatching or ready to hatch were found. In mid-April Loveridge (1936:325) found a communal nest with perhaps 50 eggs, under a log. It seemed that there were usually four eggs per clutch. Of *L. meleagris,* 14 females were found "in all stages of pregnancy" each having two eggs or embryos.

Lipinia

These viviparous lygosomine skinks are lacertiform in habitus and resemble *Leiolopisma* in most respects; they occur in southeastern Asia and islands of the southwestern Pacific northeast to the Hawaiian Islands. In the equatorial climate of New Britain Hediger (1934) found only one embryo per female in the moth skink, *L. noctua*. But in the Hawaiian Islands Oliver and Shaw (1953:91) found two embryos in each of six females while two others had only one each. Females from the Marshall, Tuamotu and Marquesas Islands also were found to have either one or two embryos. In the Hawaiian Islands, all seven females collected in September contained embryos but four females in July were not gravid.

Lygosoma

This genus includes slender, elongate, burrowing or secretive skinks in which the limbs are relatively minute. They are found from southern Asia to Australia. M. Smith (1935:291) wrote that a captive female of *L. quadrupes* in Bangkok, Thailand laid three eggs on May 27 and these hatched on June 28.

Mabuya

The grass skinks are primarily tropical in distribution but occur both north and south of the tropics and are found in both the New World and the Old World. Some are oviparous; many others in various parts of the world are viviparous. The general trend seems to be toward a long breeding season or year-round breeding in the tropics and a relatively short spring breeding season farther from the equator.

Mabuya alliacea.—A female collected by me at Pandora, Limón Province, Costa Rica, on March 11, 1965, contained a fetus that was almost fully developed. Taylor (1956:302) mentioned a specimen (KU 34339) from Costa Rica that contained several nearly full term embryos.

Mabuya aurata.—In Iran, Anderson (1963:464) recorded a female five-striped grass skink that contained eggs on May 23, 1958. M. Smith (1935:263) stated that the species is viviparous.

Mabuya bayonii.—In Angola, Manças (1963:234) noted five gravid females in September, October, and November. One had four embryos and one had seven.

Mabuya bocagi.—In Nyasaland, Loveridge (1953:208) observed mating in nature on August 12 and 24. A female that he obtained on August 10 contained minute embryos.

Mabuya brachypoda.—Webb (1958:1312) studied a series of these viviparous grass skinks from southern México, and found that births occur in late June and July. Ten containing embryos were collected from June 26 to July 28; their litters ranged from four to six. Davis and Dixon (1961:49) found that of four adult females taken near Chilpancingo, Guerrero, from June 21 through July 2, one had recently given birth and the other three contained two, three, and four embryos that were nearly full term.

Mabuya capensis.—FitzSimons (1943:218) wrote that about ten young are produced in late summer by this South African skink.

Mabuya carinata.—M. Smith (1935:268) stated that in the Godavari District of India breeding occurred in March. McCann (1940:55) noted that young were numerous in June and July.

Mabuya dissimilis.—M. Smith (1935:262) stated that this species of northwestern India is oviparous and lays six or seven eggs.

Mabuya irregularis.—Loveridge (1936:320) noted one from East Africa that contained five almost fully developed embryos on December 28, 1933.

Mabuya lacertiformis.—In Nyasaland, Loveridge (1953:202) recorded that a female obtained on January 6 contained large eggs. Many others collected the same month were obviously gravid but were not dissected.

Mabuya mabouya.—In British Guiana, Beebe (1945:31) recorded the birth of a litter of four young on August 29, 1920, and he found this species in breeding condition in July and August.

Mabuya macularia.—M. Smith (1935:266) stated that a captive female in Thailand laid three eggs, and he cited a statement by Blanford that breeding occurred in May in the Godavari district of India. McCann (1940:55) recorded a pair copulating at Salsette Island on June 22. The female of this pair contained four eggs, and another contained three. In West Pakistan, Minton (1966:100) noted, "Females from July through September are heavy with eggs. A few unattended clutches of four to six eggs presumed to be of this species were found under piles of decaying grass during July and August. Small young have been observed from late June through early October."

Mabuya maculilabris.—In tropical East Africa, Loveridge (1936:311; 1942: 344) recorded females with eggs ready to be laid on November 29 and June 17 to 20; in February he noted females with both small and large ova. Clutches contained five and 13 eggs. In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman and Chapman (1962:423) examined 14 adult females; the two from July each had shelled eggs in their oviducts, and others from June (2), September (1), and October (1) had enlarged ova 8 to 10 mm in diameter. Two each from May and November had enlarged oviducts indicating recent parturition. A long breeding season is indicated.

Mabuya megalura.—Loveridge (1936:315; 1942:346) recorded seven gravid females collected in East Africa in the latter half of February of two different years. They contained 4, 4, 5, 6, 6, 8, and 13 eggs or embryos.

Mabuya multifasciata.—Taylor and Elbel (1958:1108) reported a gravid female with nearly full term embryos in Thailand on July 28, and reported recently born young on May 16. A long breeding season, with the possibility of at least two litters per female per season, is indicated. In equatorial rain forest at Nanga Tekalit in Borneo, Inger and Greenberg (1966:1017) obtained four gravid females, three of which each contained three eggs, while the other had only two. The same authors recorded a specimen from Assam that contained six eggs, and cited statements of clutch size as four to eight, or five to seven eggs on the Asiatic mainland farther from the equator.

Mabuya quinquetaeniata.—Schmidt and Inger (1957:130) wrote that the African five-lined skink lays about 10 eggs under stones or logs, and as many as 40 have been found under one log, but in different stages of development indicating that different females had contributed to the lot. In Nyasaland, Loveridge (1953:198) reported a female containing large oviducal eggs in August. Loveridge (1936:316) reported a female containing oviducal eggs in late April. According to FitzSimons (1943:215), in South Africa six to eight young are born in late summer, and if this statement is correct it indicates a shift to viviparity in the cooler climate of the southern part of the range.

Mabuya rudis.—In equatorial rain forest of Nanga Tekalit in Borneo, Inger and Greenberg (1966:1015) obtained gravid females in six months of the year, and at least one gravid female was obtained in every month in which the sample exceeded one. Nine gravid females each contained two eggs, nine each contained three, and one contained four.

Mabuya striata.—Robertson, Chapman and Chapman (1964:317) studied the reproductive cycle of this viviparous species in the Rukwa Valley of southwestern Tanganyika only a few degrees (6° to 9°) south of the equator. Evidence from the male and female gonads and from the incidence of young indicated that there was some breeding throughout most of the year, but with a marked depression from August to October. A total of 117 skinks was examined. The percentages of the adult females that contained embryos in each month were as follows: January 0, February 18, March 87, April 85, May 75, June 68, July 35, August 60, September 22, October 20, November 10, December 0. Young less than 59 mm in snout-vent length were absent in February, March, and April, but increased rapidly in May and June to a peak in July, then tapered off gradually to a small number in December. In 90 gravid females eggs or embryos averaged 7 (2 to 11). In the equatorial region where this study was made, extent of breeding activity is seemingly controlled by the abundance of insect prey and this in turn is influenced by the amount of rainfall. The rainy season brings a great abundance of insects.

Limited data from other parts of the range indicate that breeding schedules may be somewhat altered in response to local climates. Loveridge (1929:77) stated that a female from Mombasa in East Africa had advanced embryos on June 24. In later papers the same author (1936:319; 1953:204) recorded gravid females on January 19 and February 10, and he noted that many, possibly all, females collected in Nyasaland in January were gravid. Different females contained 6, 6, 6, 6, 6, and 9 eggs or embryos. Pienaar (1966:67) stated that in Kruger National Park, South Africa, the five to 10 young are born in late summer or autumn, but he mentioned females from Southwest Africa bearing well developed embryos in midwinter. In adjacent Angola, Manças (1963:235) noted females with 3, 4, 5, and 7 eggs in August, September and October.

Mabuya sulcata.—In this South African species mating occurs in spring, and about four young per litter are born in late summer (FitzSimons, 1943:228).

Mabuya unimarginata.—A series of 36 in the University of Kansas Museum of Natural History from the Pacific slope of Costa Rica were examined. All but one, for which dates were recorded, had been collected in July and August, and these comprised two fairly distinct size groups: adults 76 to 80

mm snout-vent, and young 56 to 60 mm. One female obtained August 22 or 23 contained two ova 3 mm in diameter; five others had enlarged oviducts suggesting recent birth of litters.

Mabuya varia.—Loveridge (1936:318; 1942:347; 1953:214) published notes on the reproduction of this wide-ranging species, from various parts of East Africa. He reported gravid females March 11 to 18 (one giving birth), March 23, April 16, August 2 to 5, August 8 to 20, September 2 to 7, September 27, October, and November 30. Unborn litters of 1, 2, 2, 3, 4, 4, 6, and 8 young were reported, and in another group the numbers ranged from four to six. FitzSimons wrote that in South Africa four to 12 young are born in late summer.

Mabuya vittata.—Mosauer (1934:56) examined females in Tunisia and observed that series collected in Tozeur, April 30 to May 11, and at Gafsa June 1 to 5 contained partly developed embryos.

Melanoseps

These are limbless fossorial skinks of tropical Africa. In Nyasaland Loveridge (1953:222) found that in *M. ater* ". . . almost all females taken between mid-September and mid-October were gravid, usually holding about three elongate eggs, very approximately 10 × 5 mm, some of which contained tiny embryos."

Mochlus

These small lygosomine skinks of eastern Asia and Africa are elongate but retain well developed limbs. Loveridge (1936:322-323) observed that females of *M. modestus* from Voi, East Africa were gravid in early June, each containing two eggs or rarely three. He reported East African females of *M. sundevalli* gravid in mid-June; one had four eggs, the other had six. In South Africa FitzSimons (1943:235) found breeding at just the opposite time of year, with the clutch, usually of four eggs, produced in late summer. Gans, Laurent and Pandit (1965:38) reported a female of *M. vinciguerrae* taken alive, near Agfoi, Somali Republic, which gave birth to one young on August 5, 1961, and was found to contain two others.

Neoseps

This is a monotypic genus of small Floridan skinks in which the body is elongate, the limbs, especially the front pair, are greatly reduced, and the eyes are small. Telford (1959:110-119) studied the life history of *N. reynoldsi*. Mating occurs in March and April. In one instance a female laid a clutch of two eggs 55 days after mating. Two others also have been recorded to have contained clutches of two unlaid eggs. Seemingly sexual maturity is attained at the end of the first year.

Nessia

This is a Ceylonese genus of small, elongate, fossorial skinks having much reduced limbs. M. Smith (1935:356) stated that *N. burtoni* is oviparous, with two eggs constituting a clutch.

Ophiomorus

These are elongate, fossorial skinks in which the limbs are small with the number of digits reduced, and the head is wedge-shaped with the jaw countersunk. Minton (1966:106) reported that a female of *O. tridactylus* collected near Sanghar, West Pakistan, on April 1, contained four small embryos with large yolk masses, and he collected small young near Karachi in late June.

Ophioscincus

These are small, limbless, vermiform, fossorial skinks occurring in southeastern Asia and Australia. In Thailand, Taylor (1963:1060) found a single newborn young of *O. roulei* on April 21 in a terrarium with a female captured a few days before. Taylor noted that other females collected at the same time contained embryos in different stages of development.

Riopa

These viviparous vermiform lygosomine skinks of southern Asia and tropical East Africa have the limbs much reduced. Loveridge (1936:321) examined 14 *R. tanae* from Kan, East Africa, on June 4 and found most of the females to be gravid, with either two or three embryos.

Saiphos

These oviparous, elongate lygosomine skinks occur from southeastern Asia to Australia. Bustard (1964:715) reported that a female *S. equalis* from near Dorrigo, New South Wales, Australia, laid three eggs in early March.

Cogger (1967:74) stated that *S. equalis* represents an intermediate stage between the skinks that are typical egg-layers and those that are live-bearers; when its eggs are laid they contain advanced embryos which complete their development and hatch within a few days.

Scelotes

These small, elongate, snakelike, viviparous skinks of Africa and nearby islands in the Indian Ocean, tend to have limbs much reduced or absent. Fitz-Simons (1943:183 and 205) writing of the South African species, noted that a female of *S. alberti* had five well developed embryos in mid-December and that in *S. mira,* young, usually four, are born in the latter half of summer. He noted that in *S. bipes* there are only two per litter, born in March. Rose (1929:127) also noted two young of this species born in March. Pienaar (1966:57) stated that in *S. bidigittatus* one or two young are born in late summer or early autumn. Loveridge (1942:359) reported that five females of the East African *S. tetradactylus* had small eggs in mid-March but a sixth had oviducal eggs.

Scincella

This genus includes the few lygosomine skinks found in North and Middle America. Other species are found in Australia, Asia, and neighboring islands.

The species are so similar to those of *Leiolopisma* that they are separated with difficulty.

Scincella assata.—In Chiapas, México, Alvarez del Toro (1960:109) found that the female lays two to four eggs, from May to July. At Chilpancingo, Guerrero, México, in the latter half of June, Davis and Dixon (1961:50) found that most females were gravid, containing one to four eggs. Seemingly the population consisted essentially of adults at that time of year.

Scincella cherrici.—Greene (1969:55) examined 90 specimens in the University of Kansas Museum of Natural History from Central America representing the months of March through September; he concluded from the seasonal distribution of ovarian follicles, oviducal eggs, and hatchlings that breeding extends over this entire period. Of the 25 adult females examined, 24 per cent were gravid. On March 5 and 6, 1965, I collected a series of 20 in the Atlantic lowlands at Puerto Viejo, Heredia Province, Costa Rica. All of five adult females were gravid. Also, there were hatchlings and larger young, of the following snout-vent lengths: 22, 23, 23, 26, 27, 32, 33, 44, 44, 48, 51. Although the period of gestation and the growth rate are unknown they may be assumed to resemble those of *S. laterale*, and extrapolation suggests that these young must have been produced by mothers who were gravid in several of the months (October through February) not included in Greene's records. A year-round breeding season is probable, although more records are needed to demonstrate with certainty that breeding continues through the autumn and winter.

Of the five adult females examined by me, two each contained two eggs and the other three each contained three. Greene wrote that each of four females containing oviducal eggs had two. A small average clutch of only 2.25 eggs is indicated by this small sample.

Scincella himalayanum.—M. Smith (1935:300) stated that this montane species is viviparous, producing three or four young at a time, and that gravid females were found in May but not in September.

Scincella laterale.—The ground skink, common in the southeastern United States, is one of the smallest North American lizards; its eggs are laid with embryonic development already well underway; the female does not remain to guard her clutch as in *Eumeces,* but may rapidly recuperate and produce additional clutches of eggs in the course of the same season. Anderson (1965:95) wrote that "A Greene County [Missouri] female laid a clutch of four eggs on May 31 and a second clutch of three eggs on June 22." This is the only definite information available regarding the interval between clutches, but probably the 22-day interval Anderson recorded is near the minimum. At the northern end of the range, as in northeastern Kansas, egg-laying extends from some time in April into July; two broods per season may be typical, but farther south on the Gulf Coast, egg-laying probably extends from early April through the first half of August, and as many as five clutches per female seem possible. Known incubation periods range from a little less than a month to a little more than two months. Females are not known to attain sexual maturity in the same season in which they are hatched. Some, hatched relatively early, are breeding adults by the following spring. Others hatched later in the season (especially in the northern part of the range) emerge from their first hibernation still less

than halfgrown. Fitch and Greene (1965:572) found strong correlation between number of eggs per clutch and average snout-vent length of females (130 in all), as follows: 1 egg—♀ 43.3 mm, 2 eggs—♀ 44.6 mm, 3 eggs—♀ 47.0 mm, 4 eggs—♀ 49.4 mm, 5 eggs—♀ 50.5 mm, 6 eggs—♀ 52.6 mm, 7 eggs—♀ 52.0 mm.

Average clutch size varied in several geographic samples as follows: 2.97 in 130 females from over the entire range but chiefly from the western part; 3.77 in 31 females from Kansas and Missouri; 2.35 in 17 females from Arkansas and Oklahoma; 3.02 in 57 females from Texas; 2.82 in 11 females from the vicinity of Houston (Lewis, 1951:235); 3.3 in 31 females from Louisiana (Johnson, 1953:19); 2.6 in a sizeable but unspecified number of clutches from northern Florida (Brooks, 1967:79).

In an intensive population study on a small area at Gainesville, Florida, Brooks found that oviducal eggs were present from April through August. In males testes began enlarging in October, and reached a maximum size in January; then there was gradual decrease, to a minimum in August.

Scincella reevesi.—Webb, Jones and Byers (1962:163) reported one in Korea that contained "enlarged" follicles 1 mm in diameter on October 23. Obviously ovulation would not have occurred until the following spring. The same authors mentioned a male that had enlarged testes, possibly indicative of breeding activity, on August 10.

Scincella sikkimense.—M. Smith (1935:302) reported the finding of two clutches of eggs at 4700 feet in the last week of June.

Sphenomorphus

These small, terrestrial or arboreal, lacertiform, tropical lygosomine skinks occur from southeastern Asia to the Papuan, Melanesian and Australian regions. Most species seem to be viviparous. Worrell (1964:53) wrote that *S. quoyi* of South Australia is viviparous, producing about eight young in a litter. Brongersma (1942:134) obtained 22 gravid females of *S. temminckii* from West Java; the dates of collection were not recorded. Eggs averaged 3.4; 11 had two, four had three, four had five, and three had seven. Bustard (1964: 175) reported the birth of five young on March 7 to a female of the Australian skink, *S. tryoni,* an inhabitant of tropical rain forests. Loveridge (1948:353) reported that a female of the New Guinean *S. pratti* contained three oviducal eggs on June 13. Cogger (1967:72) stated that the Australian copper-tailed skink, *S. taeniolata,* is oviparous whereas the desert banded skink, *S. fasciolatum* is a live-bearer. Taylor (1963:1024) noted that in *S. indicus* there are six to nine young per litter.

Tiliqua

The blue-tongues are large, heavy-bodied, smooth-scaled viviparous Australian skinks. Worrell (1964:62-63) wrote that in *T. scincoides* the litter consists of about six to 20 young. *T. casuarinae* has about six young, *T. gerrardi* 12 to 24. Waite (1929:144) stated that the young of *T. scincoides* are born in the warmer part of the year in South Australia. For this species Tschambers

(1949:141) cited literature records of litters numbering 10, 14, and 18 young, and he recorded birth of two litters, of five young each, at the Lincoln Park Zoo in Chicago. One litter was born on January 15 some two months after the lizards were received from Australia.

Trachydosaurus

The stump-tailed skinks are large, armored, heavy-bodied, keel-scaled, viviparous, Australian lizards. Waite (1929:140) wrote that *T. rugosus* has only two young per litter. The young are relatively large at birth, approximately half the length of the mother.

Tropidophorus

The waterside skinks are viviparous lizards occurring from southeastern Asia to northern Australia. In equatorial rain forest at Nanga Tekalit, Borneo, Inger and Greenberg (1966:1017) obtained 16 gravid females of *T. brookei*. Five each contained five eggs, eight each contained four, two each contained three and one contained one. Smith (1935:329) reported that two females of the Indian *T. microlepis* which he kept gave birth to seven and nine young, respectively, at the end of April.

Typhlosaurus

These are elongate limbless vermiform South African lizards in which the eyes are vestigial. Brain (1959a:71) examined two females of the highly fossorial *T. lineatus* of the Kalahari Desert on February 20, 1958. One female 138 mm in length contained a fetus of 71 mm and the other female (137 mm in length) had a fetus of 74 mm. The young are thus relatively large at birth, and a remarkably low reproductive potential for a lizard is indicated.

Cordylidae

These are medium-sized, viviparous, African lizards that are usually saxicolous in dry, open habitats. *Chamaesaura anguina* is a serpentiform South African species having much reduced limbs. FitzSimons (1943:412) stated that the four or five young are born in late summer.

Cordylus is a large genus, the girdle-tailed lizards, mostly living in eastern and southern Africa. One litter per year per female is the rule, and there are one to four young. FitzSimons (1943:420-457) made the following statements concerning South African species: *C. cordylus*—one to three young, most often only one, which is born in late summer; *C. cataphractus*—young born in summer; *C. coeruleopunctatus*—females with three and four late embryos in late November; *C. giganteus*—usually two young in late summer or autumn; *C. jonesi*—two to four young born in summer;

C. namaquensis—mating in early spring (August or September) and young born in January; *C. polyzonus*—mating in early spring and young, usually two, born in midsummer or late summer. Bustard (1955:8, 1957:71) reported that a female *C. cordylus* gave birth to young in March, and that three females of *C. polyzonus* gave birth in April. In Kruger National Park, South Africa, Pienaar (1966:94, 104, 106) found that *C. warreni* produces two to five young, usually in the latter half of summer; the montane *C. vandami* produces up to six young in January or February; and juveniles of *C. laevigatus* are in evidence during December and January. Loveridge (1936:298) found females of *C. tropidosternum* to be gravid on March 12, 1934 near Kaimosi, East Africa.

Pienaar (1966:115) stated that in *Platysaurus intermedius* the young, usually two, are born in late summer. FitzSimons (1943: 466, 469, 473, 480) stated that in *P. capensis* the one or two young are born in spring or early summer, and that in *P. guttatus* there are usually two, born in late summer. In *Pseudocordylus microlepidotus,* there are usually four young, born in late summer; in *Pseudocordylus subviridis* females collected in November had early embryos; in January embryos were almost full term.

Gerrhosauridae

This is an African and Madagascan family with several genera related to the skinks and lacertids and intermediate between them in some respects. Insofar as known they are oviparous. The plated lizards, of the genus *Gerrhosaurus,* are medium-sized to large terrestrial and saxicolous lizards occurring over much of Africa south of the Sahara Desert. Loveridge (1942:341; 1953:224, 227) published field notes concerning several of the species. A female of *G. flavigularis* from Nchisi, East Africa, contained four oviducal eggs on December 11. Eight other females collected in January and February contained only small ova, but a clutch of five eggs was found on February 10. Females of *G. major* contained only small ova in June and July, but one collected in August contained three oviducal eggs. On the coast of Kenya evidence of a definite breeding season was found, as many hatchlings of *G. nigrolineatus* were observed between May 8 and June 20. FitzSimons (1943: 271) reported that in the South African *G. validus* the clutch of four eggs is laid about midsummer.

Teiidae

This large family of lizards is confined to the New World, and most abundant in the tropics, although species occur from the northern United States to Chile and Argentina. Insofar as known all are oviparous; there are cursorial, scansorial, semi-aquatic, and fossorial types. Much information is available regarding reproductive cycles in *Cnemidophorus*, the only genus that invades the Temperate Zone of North America, but relatively little is known regarding other genera. *Cnemidophorus* breeds in spring and early summer. It is one of the few vertebrate genera in which parthenogenesis is known to occur regularly. In some other genera that are confined to the tropics *(e.g., Kentropyx, Neusticurus, Proctoporus)* breeding possibly is continuous throughout the year.

Ameiva

These are medium to large terrestrial teiids that occur in a variety of habitats in Mexico and tropical Central and South America. Available information suggests that their breeding is seasonal in some parts of Central America, but in equatorial regions there is probably year-round breeding.

Ameiva ameiva.—Beebe's (1945:12) observations on this species in British Guiana and Venezuela suggested that breeding continued through much of the year. Beebe examined the following numbers of females with eggs nearly ready to be deposited in March (2), May (2), June (3), July (3), and October (2). In March, 1967, I had the opportunity to observe the species at a locality some 1200 miles farther west but also near the equator—Santa Cecilia, Napo Province, Ecuador. At this locality the lizards were abundant on an island in the Río Aguarico, connected with the adjacent mainland at times of low water, and having various types of seral vegetation, with open areas of sand and shingle. On this island most of the lizards seen were juveniles and although 63 collected formed a graded series from hatchlings to large adults, young 40 to 50 mm in snout-vent length (judged to be not more than a month old) constituted by far the most numerous size group. Away from the island the lizards were seen only occasionally—in seral partly open situations such as in banana groves, or at edges of the air field—and all those seen were adult or subadult. None of the large females collected (121, 105, 103, 90, and 90 mm in snout-vent length) were gravid.

In June, 1966, Charles Fugler made a smaller collection in the same general area, and the composition of the population then was strikingly different. The collection consisted chiefly of adults and subadults (18) with four of intermediate size and no small young. One of the two adult females was gravid. Although inadequate to show the trend of breeding over the year, the two collections do indicate probable egg-laying in June or July, and in January and the months preceding. Also, they indicate changes in the incidence of breeding at different times of year.

Ameiva festiva.—I examined 86 specimens in the University of Kansas Museum of Natural History from Costa Rica, most from the humid eastern lowlands. Four were collected in March, one in June, 32 in July, 30 in August and 20 in September. The lone June specimen was less than half grown. There were gravid females in the collections from the other four months, as follows: one of two adults (85 mm or more snout-vent) in March; two of eight in July; five of seven in August; and five of seven in October. Young less than 60 mm in snout-vent length and probably only a few weeks old were present in the samples as follows: three of five in March; five of 32 in July; five of 30 in August, and six of 20 in September. Young of 43, 50, and 55 mm in March indicate breeding weeks earlier, probably in January; thus breeding is demonstrated to occur from early in the year into September, and may occur also in the period October to December not represented in the records. Among six of the gravid females four each contained three eggs; another had four and the remaining individual had one.

Smith (1968:238-239) in a field study at Pandora, Limón Province, concluded that there was no seasonal variation in reproduction. He examined 87 gravid females and found an average of 2.2 eggs per female. Findings were essentially similar for the present species and for *A. quadrilineata* in the same locality.

Ameiva quadrilineata.—A population study of this Central American lizard was made at Tortuguero, Limón Province, Costa Rica, by Hirth (1963a). He found juveniles on the beach in all months when observations were made, including January, February, March, April, June, July, August and September. Therefore he concluded that some breeding occurs throughout the year, but with a definite peak, as young were more abundant in August and September than at other times. Hirth measured the growth made by marked individuals, which decreased from a gain of six mm (snout-vent) per 15 days in hatchlings to less than one mm per 15 days in adults. The growth rates recorded suggest that females might reach the minimum size of sexual maturity (48 mm snout-vent) in somewhat less than three months. Probably most breeding is by first-year individuals as there is rapid population turnover. In 18 gravid females there were from one to four eggs with a mean of two.

In his study at Pandora, Limón Province, Smith (1968:238-239) concluded that for both *A. quadrilineata* and *A. festiva* reproduction occurs throughout the year, but his actual field observations were limited to a two-months period between mid-July and mid-September in 1963 and 1964. All of 96 mature females contained either yolked follicles or oviducal eggs and/or corpora lutea, with averages of 2.05 for follicles and 2.07 for oviducal eggs and corpora lutea. Captive females laid their eggs 17 to 21 days after ovulation (as determined by palpation). After laying, four to six weeks elapsed before deposition of yolk in eggs of the next clutch began.

Ameiva undulata.—Fifty-one in the University of Kansas Museum of Natural History from Yucatán (mostly from Pisté), México, were examined. All were collected in a seven-day period, July 18 to 24. There were no hatchlings, juveniles, or even halfgrown individuals. Males ranged from 85 to 115 mm snout-vent but half of them were 105 to 110 mm long. Females ranged from 76 to 103 mm in snout-vent length; five of them (76, 82, 86, 93, and 94 mm snout-vent) were nongravid, but the remaining 14 (89 to 103 mm) were

gravid. Seemingly a breeding season had begun in early July or June, after several months interruption of breeding—a time sufficient to allow the last hatchlings to grow to adolescent size of 76 to 94 mm. Presumably summer and fall constitute the breeding season on this part of the Yucatan Peninsula. Three females each contained seven eggs, three contained five, and there was one each with six, four, and two eggs.

Anadia

These minute, slender, and elongate teiids have narrow heads and much-reduced limbs. They are arboreal. Dunn (1944:18) reported two eggs of *A. bogotensis* found under a stone near Bogotá, Colombia, on October 17, 1943. These eggs were kept and hatched on December 25.

Bachia

This is a genus of tropical, wormlike, fossorial teiids in which the legs are much reduced. Beebe (1945:13) reported that a female of *B. flavescens* taken in British Guiana on June 22, 1920, contained an egg nearly ready to be laid.

Cnemidophorus

This is a large genus of terrestrial and cursorial teiids, characteristic of open habitats, from the northern United States southward into South America. Even the northern species have a breeding season that lasts for several weeks, with the potentiality for two clutches annually per female. Southern species in regions having long, hot summers, are much less in evidence after a few weeks of intensive activity in spring, and may aestivate after a fairly short breeding season. Thus all species seem to conform more or less to a seasonal breeding schedule, with egg-laying extending from April to August in some instances. Several clutches of eggs may be produced in a single season by females in populations inhabiting equable climates. From one to seven eggs comprise a clutch, but most often there are two or three. The most notable aspect of reproduction in this genus is the existence of many separate populations that seem to be parthenogenetic. In certain localities males are rare, and in others careful search has failed to reveal any males at all. Many of the species are normally bisexual, however.

Cnemidophorus angusticeps.—Maslin (1963:19) collected this species in Yucatán, México, between mid-June and mid-July, 1959. Among 62 males and 60 females there were only two juveniles (41 and 39 mm snout-vent).

Cnemidophorus communis.—On the Tres Marias Islands, México, in late March and early April, 1954, Zweifel (1959:81) found active juveniles to be abundant, but only one adult was found, and this one was inactive, beneath a stone.

Cnemidophorus costatus.—Zweifel (1959:95, 101, 105) who reported this species as *C. sacki,* obtained several records of breeding in western México. In Sinaloa and southern Sonora gravid females were recorded on July 18 (2) and 19; August 5 (3), 10, 11, and 22. In Jalisco, Tanner and Robison (1960: 59) found two freshly laid clutches on July 8; a gravid female was with one

clutch. Zweifel observed that at the Tres Marias Islands in late March and the beginning of April, 1957, only juveniles were active and the one adult found was cool and inactive beneath a stone. Near Chilpancingo in the latter half of June and early July, Davis and Dixon (1961:52) found most females to be gravid; those that were relatively small (60 to 70 mm snout-vent) contained two to four eggs, whereas the larger adults (79 to 90 mm) usually had four to six eggs.

Cnemidophorus cozumelus.—Maslin (1963:18) collected 78 in the Yucatan Peninsula, between mid-June and mid-July, 1959. All were females; seemingly this species is parthenogenetic. Fourteen of the lizards contained large, nearly mature eggs, and 12 others had slightly enlarged eggs (up to 3 mm) but most had immature ovaries. Maslin suggested that there might be several broods per season, judging from variation in size of the lizards and in degree of development of ovaries.

Cnemidophorus deppii.—In Morelos, México, Davis and Smith (1953:106) collected a female having two shelled eggs in her oviducts on August 21. On the same date another female had two ova 4 mm in diameter. Between July 29 and August 21 three other females had four ova each, averaging about 5 mm in diameter.

In late March, 1965, I observed these lizards at Playas del Coco, Guanacaste Province, in northwestern Costa Rica. Most of those seen were young a little more than halfgrown. I have examined 96 from Nicaragua and Costa Rica. Eighteen collected in April were adults and subadults, 61 to 80 mm snout-vent. Only three were females; they were 64, 64, and 61 mm snout-vent, and none was gravid. In a June sample eight of 11 females were gravid and in July three of six were gravid. One a little above hatching size was collected on June 27 and another, recently hatched, on August 14 and 15. Seemingly egg-laying occurs through much of the year.

Cnemidophorus exsanguis.—In the Santa Rita Mountains of southern Arizona, Echternacht (1967) found that females with mature eggs or yolked follicles were present continually between June 20 and August 18. The average clutch consisted of three eggs; the range was from one to five.

C. exsanguis is parthenogenetic; males have not been found. At the Río Conchos in northern Chihuahua, México, Smith, Williams, and Moll (1963: 210) found three small young (37½, 45, and 50 mm snout-vent) on August 17 and 18, but the population seemed to consist mainly of sexually mature females.

Cnemidophorus guttatus.—I examined 62 of these lizards in the University of Kansas Museum of Natural History from Veracruz and Guerrero, México (subspecies *guttatus* and *immutabilis*). Adult males outnumbered adult females nearly two to one. The following adult females were gravid: all three collected in June; four of five collected in July; one of two collected in August. The remainder of the year was represented by only two specimens in May and four in October. Perhaps there is partial or complete hibernation during late autumn, winter, and early spring even in the subtropical region where this species occurs. The June collection consisted of two size groups: nine well-grown young, 59 to 76 mm snout-vent, probably from the preceding summer, and 13 adults 93 to 116 mm snout-vent. The only juvenile near hatchling size

(43 mm snout-vent) was collected on October 22. Thus the breeding season extends at least from June through August, and probably begins in May or earlier. Old females probably produce several clutches per season, and yearling females probably mature in time to produce at least one clutch. Four gravid females each contained three eggs, two each contained four eggs, and one had only a single egg.

Cnemidophorus hyperythrus.—Bostic (1966) studied the reproductive cycle of this chaparral-dwelling lizard in San Diego County, California, and adjacent México in Baja California. He found that sexual maturity is attained late in the first year. Ova begin to accumulate yolk about mid-May. Fully adult females ordinarily deposit one clutch of eggs in June and another in mid-July, but for first-year females a single clutch is the quota for the season. Clutches average about 2.3 eggs.

Cnemidophorus lemniscatus.—In British Guiana and Venezuela, Beebe (1945:19) obtained evidence of continual breeding, but most activity was during (or at the end of) the rainy season. His records were for January (1), March (1), May (2), June (5), July (3), August (3), September (1), October (1). Females containing eggs were collected on January 13 and September 10.

Cnemidophorus sacki.—Davis and Smith (1953:106) reported this species as *C. gigas* and noted that only one of 17 females taken in Morelos, México, in late July was gravid.

Cnemidophorus sexlineatus.—In northeastern Kansas a local population of six-lined racerunners was studied (Fitch, 1958) over a nine-year period. Emergence from hibernation occurs in late April or early May. Some of the emerging young are only slightly larger than hatchlings and some are nearly halfgrown, but most fall between these extremes. By late May some females are noticeably gravid. Egg-laying occurs regularly throughout June and early July, and occasionally in August. Young emerging from hibernation in spring ordinarily mature in time to participate in breeding, but individually they contribute relatively small quotas of eggs. Eleven gravid probable first-year females (up to 64 mm snout-vent) averaged 1.8 eggs; eight probable second-year females (65 to 71 mm) averaged 3.1, and five larger females averaged 4.2. A female that has laid may produce a second clutch within three weeks, and perhaps more than two clutches per season are contributed by large old females, though specific records of such occurrences are lacking.

Size of clutch and timing of breeding may vary geographically. Brown (1956:36) in North Carolina found hatching to occur from late June to early September but with concentrations near mid-July and early August. In South Carolina, Bellis (1964:9) recorded appearance of hatchlings on July 21, 22, and 23. In southern Oklahoma, Carpenter (1959b:81; 1960a:175) found that on May 9, nine per cent of adult females were gravid and that the percentage gradually increased to 56 per cent in late July, then declined abruptly to only 14 per cent in early August. He found the average clutch to be only 2.46 (1 to 6) eggs. Brown found an average of 2.92 (1 to 5) eggs per clutch in 67 clutches from North Carolina. In western Texas Hoddenbach (1966:110) found 3.06 ± .14 eggs per clutch, with more eggs in earlier clutches, and more eggs in first-year females than in older ones. He found two clutches per season

to be typical, and reported 1.8 times as many eggs in the right oviduct as in the left. He stated that fat bodies in the posterior part of the coelome decrease in size as the reproductive season advances.

Cnemidophorus tesselatus.—This large desert species is another of those having all-female populations. In western Texas, Tinkle (1959:197) noted that in fall most of those seen were young of the year, 45 to 55 mm snout-vent. In spring these young still constituted a distinct size group, 60 to 70 mm snout-vent, readily distinguishable from the adults. Tinkle stated that the size distribution indicated most would not reach maturity until the second spring after birth. In the Río Conchos area of northern Chihuahua, México, Smith, Williams, and Moll (1963:211) did not observe hatchlings until August 28. On this and subsequent days five young ranging from 36 to 50 mm snout-vent were collected, but 57 others were apparently adult.

Cnemidophorus tigris.—This is a large, wide-ranging species characteristic of desert regions over much of the western United States and northern México. Several ecological studies of local populations have been made. McCoy and Hoddenbach (1966:1671-1672) compared reproduction in Mesa County, Colorado, and in Winkler County, Texas, in the northeastern and southeastern parts of the range, respectively. In the Colorado locality the growing season is relatively short, with only 154 frost-free days, as contrasted with 218 frost-free days in Winkler County, Texas. In Colorado emergence occurs about May 1 and egg-laying is concentrated about June 21. The average clutch has 3.4 eggs (2.9 in females producing their first clutches and 3.9 in older females), with only one laying per female per season. In contrast the lizards in Winkler County, Texas, emerge about mid-April, and their eggs develop relatively rapidly. Egg-laying is concentrated in late May and, for second clutches, in late July. The average clutch contains only 2.2 eggs (2.1 in the younger females, 2.8 in the older) and the individual mean reproductive potential is 4.5 eggs annually.

Near Phoenix, Arizona, William S. Parker (MS) studied a population by live-trapping and marking in 1965 and 1966. He found that emergence from hibernation occurred in March, and the spring population contained a high proportion of first-year young, from near hatching size to near adolescent size. By late June all these young had grown to adult or subadult size, and a new crop of hatchlings had appeared. Hatchlings continued to appear through July and August. Parker concluded that in the area of his study all females reach maturity by their second spring, and that early hatchlings may become reproductive in the year following. In 40 females Parker found an average clutch of 2.05, ranging from one to four in correlation with size of the female. He concluded that females lay at least two clutches per season, and probably three or four.

Tinkle's (1959:199) observations in western Texas caused him to believe that some individuals reach sexual maturity in their second summer after hatching, but that many do not mature until the third growing season. In my own study a total of 395 museum specimens were examined, notably a collection of 265 from 16 miles northwest of Pecos, Reeves County, Texas, on July 31 and August 1, 1962. This series shows that: 1, males grow to be slightly larger than females, since the seven largest, 88 to 93 mm snout-vent, were all males; 2, adults are most concentrated in the size range 81 to 83 mm snout-vent;

3, smaller adults including gravid females, in the size range 71 to 80 mm, and immatures of 52 to 70 mm snout-vent, are probably young of the previous year's crop. There were no hatchlings in the Reeves County collection, and many of the adult females (17 in a total of 76) were still carrying eggs. For 16 gravid females the average clutch was 2.12 eggs: 10 each had two, four each had three, and two each had one.

Most observers in other parts of the range have recorded later emergence from hibernation and later appearance of hatchlings than found by Parker in southern Arizona. Appearance of hatchlings has been recorded on July 17 in southern New Mexico, July 30 and August 3 in trans-Pecos Texas (Milstead, 1957:119), August 30 in northern Chihuahua, México (Smith, Williams, and Moll, 1963:211), and near the end of July in southern Nevada (Tanner and Jorgensen, 1963:18). Obviously the population dynamics of the species undergoes change over its extensive range, affected not only by changes in size and frequency of clutch noted by McCoy and Hoddenbach but by the length of time required from hatching to maturity.

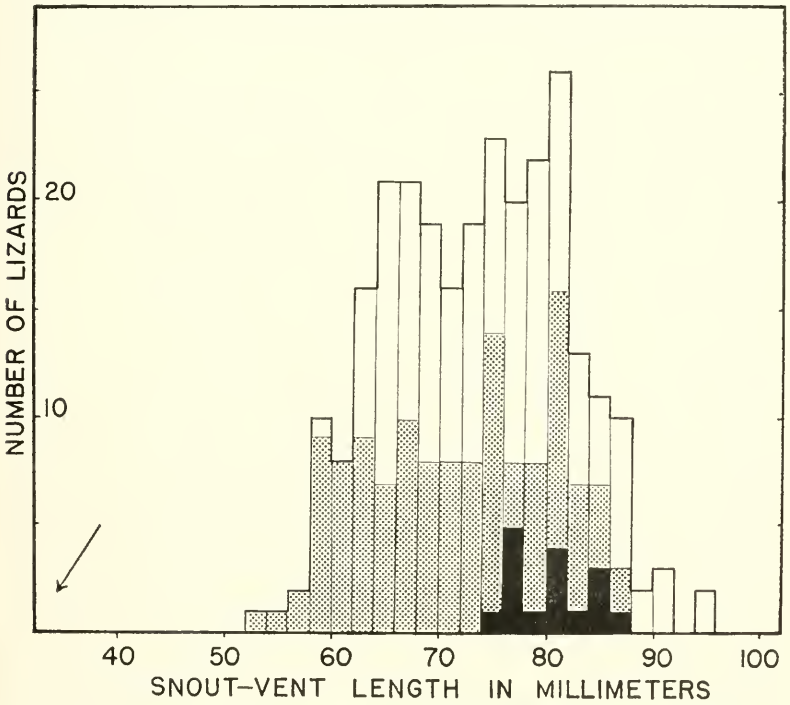


Fig. 7. Population sample of *Cnemidophorus tigris* from 16 miles northwest of Pecos, Reeves County, Texas, July 31 and August 1, 1962, based on specimens in The University of Kansas Museum of Natural History; black columns represent egg-bearing females, stippled columns represent nongravid females and open columns represent males. Young of the year had not yet appeared on the dates of sampling, but approximate size of hatchlings is indicated by arrow. Extensive overlapping in size is indicated between old adults, mostly the larger individuals, and adolescents from the preceding year's brood. It is uncertain whether the yearling females are reproductive.

Cnemidophorus velox.—Douglas (1966:732) found three to five ova in gravid females collected in Mesa Verde National Park on June 23, 1963, and June 10, 1964. Hatchlings first appeared in 1963 on August 30.

Echinosaura

These are small, secretive, partly nocturnal teiids of Panamá, Ecuador, and Colombia, often found along streams. The genus is monotypic. Uzzell (1965: 89) recorded two females of *E. horrida* each of which had two oviducal eggs, one in each oviduct.

A two-egg clutch seems to be characteristic of most microteiids *(Anadia, Echinosaura, Leposoma, Neusticurus, Prionodactylus),* although some *(Bachia, Proctoporus)* may lay only one egg at a time. Presumably the small size of the clutch is compensated for by frequent laying. At Pasto in southern Colombia, Valdivieso and Tamsitt (1963:33) collected two females of "*Euspondylus vertebralis*" (probably *Prionodactylus vertebralis*) which each contained two eggs (ovarian in one, oviducal in the other).

Kentropyx

This is a genus of medium-sized, active, rather heavy-bodied, terrestrial and scansorial South American teiids. In British Guiana, Beebe (1945:20) found a female of *K. calcaratus* that contained four eggs ready to be laid on April 18, 1924. I observed this species at Santa Cecilia, Napo Province, Ecuador, in March 1967. Of 59 that were collected, the size distribution (snout-vent length) was as follows: 30-39 mm:1; 40-49:13; 50-59:6; 60-69:3; 70-79:5; 80-89:5; 90-99:7; 100-109:14; 110-119:5. The last three groups included sexually mature individuals and there were 12 females that had oviducal eggs or enlarged ovarian follicles.

In a smaller collection made in June 1966 at Santa Cecilia and at Limón Cocha, Ecuador, by Charles Fugler, there was one gravid female, and there also were young of the following snout-vent lengths: 44, 61, 76, 82, 85. The records establish that there is egg-laying in June, also in March, and perhaps in the three or four months preceding it. Year-round breeding seems probable although records from late summer and autumn are desirable. Six gravid females each contained two eggs; four each had five, and there was one each with four, three, and one. With Beebe's record these indicate an average clutch of 3.07.

Leposoma

These minute teiids occur in northern South America and adjacent Central America.

Leposoma percarinatum.—In British Guiana Beebe (1945:21) found two clutches of two eggs each on March 6, 1922, and on April 28 a captive female laid two eggs. On June 19, 1919, a female containing two enlarged eggs was captured.

Leposoma southi.—Taylor (1956:237) mentioned two eggs found at the base of a tree, in Costa Rica. They had nearly completed incubation, and when

one of the eggs was broken the young lizard escaped. A gravid female contained two eggs, hence this was assumed to be the typical clutch. Eleven gravid females that I examined from Panamá and Costa Rica also each contained two eggs.

Neusticurus

These small teiids of tropical South America, and Panamá, live near streams and ponds, and obtain their food from the water.

Neusticurus ecpleopus.—Uzzell (1966:313) recorded two communal nests of brown water lizards, one with four and the other with five eggs, in a rotten log at the Río Iscozazín in Peru. Eggs in both nests were beginning to hatch. In 19 instances females of *Neusticurus* laid clutches of two eggs apiece, or were found to contain two oviducal eggs when dissected. A twentieth individual contained only a single egg but perhaps had already laid one.

In March, 1967, I had the opportunity to observe this species at Santa Cecilia, Napo Province, Ecuador. Forty-two were collected and approximately an equal number that were seen escaped. Twelve that were considered adults were distributed over a remarkably wide size range, from 49 to 65 mm, and the six of these that were females were all gravid. The remaining 30 were of graded sizes from hatchlings to subadults but with ten concentrated in the range 26 to 30 mm—probably in their first month of life after hatching. A single hatchling was collected in the same area by Charles Fugler in June, 1966. The season of hatching is thus demonstrated to extend from late winter through early summer, and probably extends throughout the year.

Proctoporus

These are small, ground-living South American teiids. Test, Sexton and Heatwole (1966:29) found that *P. achylens* breeds through most of the year in Estado Aragua, Venezuela. They found individuals of hatchling size in January, March, July, October, November, and December. The last month produced the largest sample and, allowing two months for incubation, may indicate that October, in the waning part of the rainy season, is a time of heightened egg-laying activity. No records of egg-laying in March were obtained, nor were there records of hatchlings in May. March is the last and driest month of the non-rainy season, and the authors suggested egg-laying might cease briefly at that time of year. Three females of *P. striatus* obtained by Valdivieso and Tamsitt (1963:34) at Bogotá, Colombia, in March 1960 each laid a single egg in a terrarium soon after capture.

Tupinambis

This South American genus includes the giants of the family—active, fast-moving predatory lizards that are mainly terrestrial but swim, climb, and dig well. In southern Brazil, Milstead (1961:26) dissected a female *T. teguixin* which contained 32 oviducal eggs averaging 23 mm in length. This same female tegu contained approximately 50 enlarged ovarian follicles (1 to 3 mm in diameter) suggesting that a second clutch would have been produced not long after the first. In British Guiana Beebe (1945:26) found a clutch of

six eggs of *T. nigropunctatus* in a termite nest on June 16, 1919, and a clutch of four eggs on April 16, 1924. He observed a mating pair on April 20, 1924, and a female containing six eggs on August 21, 1922.

Lacertidae

The lacertids comprise a sizable family of lizards, best represented in Africa, but found also across Europe and Asia, except in the far north. These are terrestrial lizards, mostly of active and cursorial habits, frequenting open situations. All are oviparous, but the northernmost species, *Lacerta vivipara,* has attained viviparity over an extensive area in the northern part of its range. Most information concerning breeding cycles pertains to species in the Temperate Zone; for them a long breeding season with production of two or several clutches of eggs by an individual female seems to be a common pattern.

Acanthodactylus

The fringe-footed lizards are essentially a desert group found in North Africa, extreme southern Europe, and southwestern Asia—areas having a pronounced winter season.

Acanthodactylus cantoris.—This is a species of Pakistan, Iran, and neighboring areas. Anderson (1963:457) noted that females carrying ovarian eggs indicate egg-laying in autumn or even in winter. He cited Blanford (1876), who found numerous young in November, and concluded that eggs hatch in autumn as no small juveniles are found in spring or summer. Minton (1966: 107) reported that females containing large eggs had been collected from late March through July, and that young began to appear about the end of June and became increasingly common through the first half of October.

Acanthodactylus pardalis.—At Sidi bon Ali, Tunisia, Mosauer (1934:53) found that females contained two to four eggs (three in most instances) on April 22, 1928.

Algyroides

This genus includes several species in Europe and Africa. Loveridge (1942: 336) reported several gravid females of the sparser-scaled forest lizard, *A. vanereselli,* from Idwi Island, Lake Kivu, Congo, in February. *A. alleni* is a montane grassland species, limited to altitudes above 9000 feet on Mt. Elgon in Uganda and Mt. Kenya in Kenya. Greer (1968:231) noted that *A. alleni* and two species of snakes found in the same montane grassland habitat were exceptional in their oviparity, whereas 11 other species of snakes and lizards of five families that occur there are all viviparous. Greer quoted an informant that the eggs of *A. alleni* are laid under flat stones, and he mentioned dissecting a gravid female containing two shelled eggs in which there was still no sign of embryonic development.

Cabrita

This genus includes two species of jungle-inhabiting lizards found in tropical India and Ceylon. M. Smith (1935:375) reported that a female of *C. leschenaulti* contained six eggs in April, and juveniles were observed in the same month.

Eremias

This large genus of slender, active, terrestrial lacertids, occurs across Asia to southeastern Europe and through much of Africa in deserts and other open habitats. Compared with species of the closely related genus *Lacerta*, those of *Eremias* are, in general, smaller and have a more rapid sequence of generations and a relatively short life expectancy.

Eremias argus.—Webb, Jones and Byers (1962:162) studied specimens from Korea and found a female to be gravid on May 8; another female laid four eggs between June 4 and 14.

Eremias arguta.—Fuhn and Vancea (1961:258) stated that mating occurs in May and oviposition in the first week of July in Romania. Darevsky (1960: 1217) studied this lizard in Armenia. At altitudes of about 2000 meters it is active for only about 4½ to 5 months of the year; nevertheless two or more clutches of eggs are produced in the course of the season of activity. Only the first clutch develops at the expense of the fat bodies. Eggs of later clutches draw on nutrients directly as these are ingested and assimilated.

Eremias guttulata.—In Iran Anderson (1963:460) found females that contained eggs on March 2, April 7 and August 16. He observed hatchlings from late April through November. He expressed the opinion that adult size is attained in the spring following the season in which the eggs hatch. At Sidi bon Ali in Tunisia, Mosauer (1934:53) noted that females contained two to three large eggs on April 22. In West Pakistan, Minton (1966:110) obtained evidence of an early spring breeding season with young appearing as early as May and reaching maturity by the following winter.

Eremias lineocellata.—In South Africa, FitzSimons (1943:346) found that about six eggs were laid in early summer.

Eremias neumanni.—On the basis of observations at Ngatana River, East Africa, June 11 to 16, 1934, Loveridge (1936:306) wrote, "It seems possible that the main breeding season was over though half a dozen females [in a series totalling 66 specimens] were gravid." One held three eggs measuring 8 × 6 mm; another, three measuring 9 × 5; a third, two eggs measuring 11 × 6.

Eremias pleskei.—Peters (1964:467) studying this species in southwestern Asia, concluded that the young from eggs produced early in the season mature and breed before the end of their first year of life. Females generally produce two clutches of eggs per season, and clutches average two eggs each. In two to three years of life a female probably totals approximately 12 eggs. Similar patterns of development, reproduction and survival occur in *E. lineolata* and *E. scripta.*

Eremias specki.—Loveridge (1936:307) recorded gravid females and many juveniles in East Africa, March 23 to 30. There were four eggs in each of three females and five in one. On September 9, 1933, most females were gravid.

Eremias velox.—This is another Asiatic species studied by Peters (1964: 467). He found that maturity was attained at the end of the first year. In the summer following their hatching, females generally produce two clutches of eggs, but in subsequent summers, after further growth, females produce three or four clutchs per season with, on the average, more eggs than occurred in the early clutches, and sometimes as many as six eggs. The same pattern holds for *E. strauchi.* In West Pakistan, Minton (1966:109) obtained data indicating a spring breeding season, with eggs laid from late May to early July. Near Quetta young appeared in late August.

Ichnotropis

This genus includes several species of active terrestrial lizards of tropical Africa and some in South Africa. In Angola, Manças (1963:238) recorded gravid females of *I. capensis* in October and November. Different individuals contained 6, 7, 8, 9, 9, and 11 eggs. In the Rukwa Valley of Tanganyika 6° to 9° south latitude, Robertson, Chapman, and Chapman (1962:425) obtained a gravid female in July, having one shelled ovum in each oviduct, and one in July had ovarian eggs. Pienaar (1966:92, 93) writing of the fauna of Kruger National Park, but perhaps drawing upon records from other areas, stated that the clutch in *I. capensis* is usually six and that in *I. squamulosa* is usually 10 to 12.

Lacerta

This genus, common in the Mediterranean region, and extending through much of Africa and into central Asia, is most characteristic of open habitats, with cursorial adaptation and incipient scansorial habits in some. All the species except *L. vivipara* in the northern part of its range are oviparous and several are known to produce two or more clutches in a season. *L. vivipara* occurs in relatively cold climates and its viviparous habits are an obvious adaptation to cool and damp weather, but the long gestation period limits it to a single brood per season and results in reduced reproductive potential.

Lacerta agilis.—Smith (1951:188-190) summarized the facts concerning the reproduction of this species in England and France. Mating is usually in May. The eggs, usually six to 13, are laid in June and July, and require seven to 12 weeks incubation. Some females on the European mainland lay relatively early in the season, in May, and later produce second clutches. There are no records of second clutches in England. Embryonic development has already begun when the eggs are laid. In Romania, Fuhn and Vancea (1961:197 and 203) found that breeding occurs in May or June; females are gravid in early July and sometimes until August. Eggs may be laid by mid-July and hatchlings appear in late August. Kehl and Combescot (1955:58) described seasonal changes in the reproductive tracts. They stated that follicle formation continues throughout the year. The eggs maturing in April and May are discharged from the ovary. The mid-section of the oviduct with ciliated and granular epithelial

cells thickens to 120 microns in May, but is only 45 microns in August. In spring the epithelium of the anterior genital area of the fossette in the female is much thickened in adult individuals (210 to 260 microns *vs.* 35 to 40 microns in the male) and its lower aspect is pitted with tubular invaginations which enter the underlying tissue.

Lacerta jacksoni.—Loveridge (1936:301; 1942:334) published the following notes concerning the reproduction of this East African species:

December 12 to 24 ..... Two females had ova 4 × 7 mm
January 29 ..... A female had three eggs
February 10 to 28 ..... Two females each contained four eggs 14 × 7 mm and 15 × 7 mm
February 13 to 28 .... Many females (in a series of 85 specimens) were gravid, with three to five eggs ready to lay

Lacerta muralis.—In an early study of the wall lizard in the Indre district of central France, Rollinat (1897:5-23) found that mating occurs toward the end of March. During spring and early summer fat bodies undergo reduction in both sexes, but especially in females with enlarging ovarian follicles. Ovulation occurs in the latter part of April, and egg laying is chiefly in May and June. There are three to eight eggs in a clutch—usually only three in females producing their first clutches. Rollinat found that only one clutch per year was produced in the area of his study. The lizards attained sexual maturity in their fourth year. Eggs hatch from late July to September.

Cooper (1958:113) observed the reproduction of this common European species in confinement. Seven females laid their eggs on June 1, 3, 6, 12, 14, 17 and 21, respectively. Four of these females produced second clutches after intervals of 32, 28, 23, and 21 days and the last two each produced a third clutch, after intervals of 33 and 32 days, respectively. The author did not mention the sizes or ages of the females involved. In Romania, Fuhn and Vancea (1961:230) found that eggs are laid from May to July and old females may produce two or three clutches per season. They recorded hatching mainly in late July and early August.

Lacerta praticola.—In Romania, Fuhn and Vancea (1961:251) found this species to be active from April to October. Gravid females are seen in mid-June. A female in confinement oviposited on June 28 and eggs hatched on August 14.

Lacerta saxicola.—This Asiatic species is notable for having populations that reproduce parthenogenetically, and others that reproduce with a normal, bisexual pattern. Darevsky and Kulikova (1962:160) studied the species in parts of Armenia where bisexual and parthenogenetic populations overlap. In these areas sterile hybrids—females with reduced ovaries and oviducts—were sometimes found. In these hybrids, gametes differentiate but meiosis was found to proceed normally only to the early pachytene stage.

Lacerta taurica.—Fuhn and Vancea (1961:238) stated that in Romania egg-laying occurs in the second week of May and hatching is in September.

Lacerta viridis.—In the Indre district of central France, Rollinat (1900:16) found that mating of the green lizard occurs in May and egg-laying in the following weeks, sometimes as early as May 18. Both sexes attain maturity in

the third year, and these third-year individuals breed a little later than old adults. Rollinat (1900:18) recorded clutches of six to 19 eggs, and he thought that only one clutch per year was produced.

Sayer (1953:148) kept captive individuals received from Italy. He observed courtship several times in late April. The female laid 14 eggs on June 17 and they hatched on August 15. In Romania, Vancea and Fuhn (1959:76) and Fuhn and Vancea (1961:218) found that emergence from hibernation occurs at the end of March, egg-laying is in the last week of June or early June, and hatching is in August, usually in the first half. White (1957:89) found that captive females lay two clutches in a single season, and laying of the second clutch may take place about the time that the first is hatching.

Lacerta vivipara.—Smith (1951:196-198) stated that in England mating occurred in April and May and gestation lasted about three months, with most young born in July. Litters usually had five to eight young but ranged from four to 10. Young were usually dropped by the female in a moist, concealed situation, and sometimes did not escape from enclosing membranes for several days. Twenty-two months were required to attain sexual maturity, in the male at least. In the Pyrenees Mountains the species retains oviparous habits and eggs with parchmentlike shells are laid. As many as 60 have been found in one nest.

Fuhn and Vancea (1961:244) stated that in Romania breeding occurs in May and that attainment of sexual maturity requires at least three years. Fukada (1965:75) recorded pertinent facts concerning the natural history of this widespread species on Sakhalin, as follows. Breeding activity begins soon after emergence from hibernation, in early May, and continues from one to two weeks. During this interval lizards of both sexes may copulate two or three times daily, or even as many as five times. In early August two to five bluish-black, thin-shelled "eggs" are produced, but some young rupture the enclosing membranes immediately, and others usually do so within an hour.

The species is unique in being the only viviparous lacertid.

Latastia

These lacertids inhabit tropical East Africa. In late March and April at Voi, Kibwezi, and Mbololo, Loveridge (1936:304) obtained six gravid females of *L. longicaudata*; three contained three eggs apiece and the others each had four.

Nucras

These are rather slow-moving terrestrial lizards usually found in grassland habitat in tropical and South Africa. FitzSimons (1943:315) stated that the South African *N. delalandii* lays a clutch of four eggs about midsummer, and Pienaar (1966:88) stated that in *N. intertexta* also, the clutch is usually four eggs.

Ophisops

This genus includes desert lizards in North Africa and southwestern Asia. In Iran, Anderson (1963:462) recorded finding females of *O. elegans* con-

taining eggs on August 2 and 5, 1958, and in the autumn of 1960. In southwestern Asia, Peters (1964) found this species conforming to the same seasonal breeding pattern followed by *Eremias pleskei*, with young maturing at the end of their first year, and with females producing two relatively small clutches in their first breeding season, but producing three or four larger clutches in subsequent breeding seasons. In West Pakistan, Minton (1966:112) reported egg-laying in *O. jerdoni* in late July and early August and hatchlings collected from July through November.

Takydromus

This genus includes several species of slender, long-tailed lizards found in grassy habitats in southeastern Asia from the tropics northward to Japan and Korea. Loveridge (1945:67) stated that in Java the clutch of *T. sexlineatus* consists of two or three eggs laid in April and May. A more extended breeding season might be expected. The kanahebi, *T. tachydromoides,* is common in Japan and has been the subject of several intensive studies. Fukada (1965:74) summarized the known facts of its reproduction and life history in an account based largely on the work of Ishihara, done mostly with captive animals in the Kyoto area. A captive female may produce as many as six clutches in a single season. The interval between clutches averaged 17.5 days. Eggs averaged 3.6 (1 to 9) per clutch, but averaged as few as 3.0 for the smallest females (40 mm snout-vent), up to 6.0 for the largest (70 mm snout-vent).

Telford (1969) in a field and laboratory study in central Honshu, extended and supplemented these findings. Corpora albicantia were found to persist long after deposition of a clutch, seemingly for the lifetime of the lizard, and hence provided bases for measuring productivity, and also for aging individuals. Young females matured in the season following their first hibernation, and produced successive clutches averaging 2.6, 2.4 and 2.4 eggs in this first breeding season. Second- and third-year females also normally produced three clutches in the course of a season, with averages of 4.0, 4.0 and 3.4 eggs for the former and 4.4, 5.1 and 3.5 for the latter. Oviposition begins in early May and ends before mid-August. Number of eggs per clutch is correlated with age of female rather than with size as such. Of the total female sample 62.5 per cent had survived their first breeding season, 25.0 per cent had survived their second, 9.8 per cent their third, and 2.7 per cent their fourth season.

Tropidosaura

This genus consists of several species of terrestrial lizards living in montane habitats in South Africa. FitzSimons (1943:307) wrote that a female *T. gularis* taken near the end of November contained eight well developed eggs.

Varanidae

The monitors are small to large or giant-sized lizards occurring mainly in the tropics in Africa, Asia, the East Indies and the Australian region. They are active, strong-limbed, fine-scaled lizards well adapted for burrowing, climbing and swimming but not highly specialized for any of these ways of life.

Varanus

The living monitors are referred to this genus. They are oviparous and are probably the most prolific of lizards. The habit of ovipositing in termite nests has been reported in both African and Australian species. Cogger (1967:58) stated that for species occurring in southern Australia there is a definite spring breeding season extending from about September to December, the eggs hatching between December and March, but that in New South Wales emerging hatchlings have been found in early spring suggesting late summer mating, with eggs laid in autumn.

Varanus bengalensis.—In West Pakistan, Minton (1966:113) reported that females of the Indian monitor collected in July and early August contained 24 to 29 large eggs apparently nearly ready for deposition, and one female laid 19 eggs on August 4-5. Young are usually seen from late June through August.

Varanus griseus.—Minton (1966:115) reported that in West Pakistan newly hatched desert monitors had been collected in August and September.

Varanus komodoensis.—Little information is available concerning reproduction in the Komodo dragon lizard, a species that is by far the largest of any living lizards. Maleev and Darevsky (1963:24) stated, on the basis of specimens collected in July and August, that mating occurs no later than the beginning of July on the island of Komodo—a month earlier than in those kept in the zoo at Surabaja, Java. Young were thought to appear in March after the end of the rainy season. Darevsky and Kadarson (1964:1360) noted that in an adult female killed on August 26 there were oöcytes devoid of yolk, and 15 corpora lutea, indicating production of a clutch of eggs, probably in July or August.

Varanus monitor.—M. Smith (1935:403) wrote that in Burma the breeding season of the Indian monitor is in the hotter part of the year, and that in central India the eggs are laid in September. McCann (1940:57) noted that at Salsette Island in India, most young appear during the hot weather and the early part of the monsoon. He recorded a hatchling at Kurla in February and a juvenile judged to be from three weeks to a month old on May 24.

Varanus niloticus.—In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman and Chapman (1962:425) noted that an adult female taken in November and another in December each had ova beginning to develop (4 mm in diameter) but that one taken in May had no developing ova. In Nyasaland, Loveridge (1953:240) found small young to be abundant in mid-February. FitzSimons (1943:407) wrote that in South Africa the eggs, numbering 40 to 60 per clutch, are laid about midsummer in termite nests, and require as much as nine or 10 months to incubate.

Varanus salvator.—M. Smith (1935:407) stated that in Thailand eggs are laid at the beginning of the rainy season—usually in June.

Anguidae

This is a relatively small family occurring in northwestern Africa, Europe, Asia, North and South America, and the West Indies.

Most are medium-sized lizards having elongate bodies, reduced limbs, and a heavy dermal armor of bony plates. Of the genera here considered, *Abronia, Anguis, Ophiodes, Sauresia* and *Wetmorena* are viviparous, whereas *Diploglossus* and *Gerrhonotus* have both oviparous and viviparous species, and *Ophisaurus* is exclusively oviparous.

Abronia

These are large, arboreal alligator lizards of México and Central America. Presumably all are viviparous but no information is available for most of the species. Davis and Dixon (1961:52) mentioned a female of *A. deppei* at Chilpancingo, Guerrero, México, which contained enlarged ovarian follicles on June 10. Werler (1951:41) reported that an *A. graminea* from Las Vigas, Veracruz, México, gave birth to a litter of four young on April 12, 1950. Smith and Alvarez del Toro (1963:103) described *A. lythrochila* from Chiapas, México, and reported that the holotype contained 13 large eggs on July 11. These eggs had no discernible embryos; however, another individual gave birth to young on July 15, indicating a breeding season of many weeks duration. Smith and Williams (1963:22) mentioned four specimens of *A. oaxacae* from Oaxaca, México, and stated: "One of the young was born in early May, 1960, to No. 51270; the other was born to the same female in May, 1961." They did not explain whether the single young for each year was the entire complement, or whether the fourth specimen mentioned was an adult male which mated with the female in the interval between births.

Anguis

The viviparous slow-worms of Europe conform to a breeding schedule typical for Temperate Zone reptiles of relatively northern distribution, with mating in spring, gestation lasting through much of the summer, and birth in late summer or autumn. Smith (1951:175-180) summarized the literature regarding *A. fragilis,* and gave a comprehensive account of its life history. Mating activity is greatest during late April but may continue through May and early June. Males become sexually mature in their third year, but maturity is delayed in females until the fourth or fifth year. Ovulation occurs in June. The young are usually born in late August, and there are ordinarily six to 12 young per litter, but numbers range from four to 19. This species attains a remarkable longevity for a small lizard. A male already adult when captured survived for 54 years, and after 45 years he mated with a female known to be at least 20 years old. In Romania, Fuhn and Vancea (1961:265) studied the eastern subspecies *(A. f. colchicus)* and found that impregnation occurs in May and young are born in August.

Diploglossus

The galliwasps are large, heavy-bodied tropical lizards that have several species in the West Indies and Central America. Greer (1967:94-96) summarized the available literature records concerning their reproduction and

contributed many firsthand observations. He examined 12 gravid females of the Hispaniolan *D. costatus* which averaged 5.6 (3 to 9) eggs or embryos, and he cited literature records of birth of litters with three and eight young. In the Hispaniolan *D. crusculus* he found an average of 3.2 (2 to 5) eggs or embryos in eight gravid females. In four gravid females of the Jamaican *D. curtissi* he found an average of 3.3 (2 to 4) eggs or embryos, some of the latter almost full term. In four *D. pleii* of Puerto Rico he found two to four oviducal eggs with small embryos, and Schmidt and Inger (1957:164) stated that this species was a live-bearer. Ober (1968:326) reported that a female *D. stenurus* in Haiti gave birth to seven young June 4 to 6, 1963, and another gave birth to five young on May 15.

The Cuban *D. delasagra* is oviparous. Greer reported a gravid female containing two eggs that had small embryos but had well developed white shells, and he cited a literature record of an alleged male found with five eggs which he seemed to be guarding. *D. bilobatus* of Central America is also oviparous. William E. Duellman (pers. com.) found a clutch of six eggs under a log in a cafetal at Isla Bonita, Heredia Province, Costa Rica, on June 25, 1966. The eggs hatched on July 15, 1966. Taylor (1956:204) reported that a female was found brooding six eggs under a log in Costa Rica.

Gerrhonotus

The alligator lizards have elongate bodies and tails, short legs, and keeled scales. They occur in western North America and Middle America, from southwestern Canada southward to Panama. Here included in the genus are *Elgaria* and *Barisia* (Tihen, 1949). Stebbins (1958:23) proposed a realignment of their species, with all included in the genus *Gerrhonotus* but with two subgenera: *Gerrhonotus* with the species *kingi, panamintinus, multicarinatus, cedrosensis, paucicarinatus* and *liocephalus,* and *Barisia* with *antauges, coeruleus, gadovi, imbricatus, modestus, monticolus, moreleti, rudicollis,* and *viridiflavus.* Within each group the species are almost entirely allopatric, but the subgenera tend to parallel each other in their overall distribution, with large-scale geographic overlapping between their species. However, the subgenus *Barisia* occurs in relatively cool (northern, coastal or montane) habitats and insofar as known all its species are viviparous whereas those of the subgenus *Gerrhonotus* are oviparous.

Gerrhonotus coeruleus.—Lewis (1946:155) obtained a group of these lizards, subspecies *principis,* near Seattle, Washington, and noticed vigorous mating activity in several different cages containing them from April 26 to 28. Four litters were born from seven to ten weeks later, and young numbered 4, 5, 6 and 7. On the Oregon coast Pimentel (1959:6) collected 14 gravid females and found four to six eggs per female. Svihla (1942:54) observed a mating at Seattle, Washington, on April 6, and Vestal (1940:51) observed a mating in northwestern California on April 16. At the latitude of San Francisco copulation has been observed by myself and others in *G. c. coeruleus* in the second week of April. Alligator lizards are capable of activity at relatively low temperatures, and in the mild coastal climate that prevails over much of the range the season of activity is long. However, farther inland at high elevations emergence and breeding are delayed and the season of activity is much

shortened. Van Denburgh (1922:447) wrote that in Yosemite Valley these lizards mate about the middle of June; if typical, this indicates notable delay which might postpone attainment of maturity for one or more seasons and affect markedly the population structure. Where the species occurs at much higher altitudes and/or much farther north, the effect would be correspondingly greater.

Gerrhonotus gadovi.—Stebbins (1958:18) stated that a female from 8200 feet near Omilteme, Guerrero, México, contained five fetuses nearly full term on April 28. Davis and Dixon (1961:53) recorded a juvenile that could not have been more than a few weeks old at Chilpancingo, Guerrero, México, on June 24.

Gerrhonotus imbricatus.—Duellman (1961:88) mentioned finding a copulating pair on July 4, 1955, on Cerro Barolosa, Michoacán, México, at an altitude of 2700 meters. Stebbins (1958:18) mentioned a female taken in México on Cerro Popocatépetl, 11,000 feet on May 4, which contained five young ready for birth, as did another from Omilteme, 8200 feet, Guerrero.

Gerrhonotus kingi.—Stebbins (1958:22) stated that a female from Cochise County, Arizona, laid 15 eggs on June 5, 1957.

Gerrhonotus liocephalus.—This large alligator lizard of southwestern Texas and México has a short and incomplete hibernation period and a long season of activity. Flury (1949:65) observed several instances of copulation in autumn in captive individuals. He concluded that autumn is the breeding season, but perhaps breeding extends over most of the season of activity or all of it. He recorded that a captive female laid 14 eggs on March 30, 1948, and these eggs hatched on May 16, 17, and 18. A newly caught female laid 22 eggs on May 11, 1948. In the Big Bend region of Texas, Minton (1959:45) recorded a juvenile of 45 mm snout-vent length (well above the size at birth) on July 17. Werler (1951:41) wrote that at the San Antonio Zoo a female from Medina County, Texas, laid 12 eggs January 30 to February 1, 1950, and another female from central Texas laid five eggs on February 18, 1950. The latter clutch hatched from March 31 to April 2. Greene and Dial (1966:303) described brooding behavior in a female found in a rock crevice coiled around a clutch of eight eggs. Burkett (1962:211) obtained a female from Georgetown, Williamson County, Texas, which on May 15 after brief captivity, laid a clutch of 31 eggs. On or about June 9 this individual deposited a second large clutch of 28 eggs. The relatively short interval between clutches in this individual, and the wide span of egg-laying dates, suggest the potentiality for several broods per season and a notably high reproductive potential.

Gerrhonotus monticolus.—This viviparous species lives at high altitudes in Central America. I examined 65 from central Costa Rica in the University of Kansas Museum of Natural History. All were collected in July and August, except for five in March and four in June. Of the latter, two are adult females, both gravid; 12 of 13 adult females from July also were gravid. The thirteenth was of minimum adult size (63 mm snout-vent) and perhaps still sexually immature. However, in the August sample four adult females were gravid and four were not, suggesting the waning of a reproductive cycle. One female had full term embryos but in two others enlarged ovarian follicles still were not

full-sized and subsequent embryonic development would have extended for many weeks, probably through September and into October. A juvenile taken in mid-July had a snout-vent length of only 36 mm and could not have been more than a few weeks old. The female that bore it must have been gravid in spring—probably April, May and June. One of the five specimens collected in March (the 22nd) was 34 mm in snout-vent length and was judged to represent a pregnancy that may have begun in December and extended through January and February. Thus the small group of specimens at hand indicates a breeding season that extends through most of the year (December through October), but with some seasonal change and with the greatest incidence of gravid individuals in early summer. In 17 gravid females, eggs or embryos averaged 5.35 (3 to 10).

Gerrhonotus moreletii.—This is a small montane Central American species. Stuart (1948:60) wrote that in Alta Verapaz, Guatemala, this lizard bears its young about mid-May, when the heavy rains begin. In field work in 1940 he found the first newborn young on May 21, and on the same day collected a female that contained nine fully developed fetuses. Stuart (1951:60) reported newborn young at Ixchiguán, Guatemala, in early June.

Thirty in the collection of the Museum of Natural History were examined. All seven of the adult females (more than 73 mm snout-vent) collected February 24 and 25 contained late embryos. There were no small juveniles in this winter sample, but one male was below adult size (61 mm snout-vent). In a July sample of 21, four adult females were not gravid and three others contained enlarged ovarian follicles. There were juveniles of 33 and 36 mm snout-vent length (several weeks old) and other older immatures of 53, 56, 57, 64 and 65 mm. The specimen that was 53 mm snout-vent was a female already gravid, carrying three embryos, indicating that sexual maturity is attained at a remarkably small size and probably at an early age. Breeding through much of the year is indicated, but with some indication that it slackens or ceases in autumn. In 15 gravid females, eggs or embryos averaged 6.0 (4 to 9).

Gerrhonotus multicarinatus.—Fifty specimens from Oregon (subspecies *scincicauda*) and 82 specimens from southern California (subspecies *webbi*) in the Museum of Vertebrate Zoology were examined to determine the breeding cycle and to search for possible differences in schedules existing between populations in the northern and southern parts of the range. Nine of ten adult females (120 mm or more snout-vent) from Oregon in May and June contained enlarged ovarian follicles. Other adult females collected on July 5, 17 and 19 did not have enlarged follicles and probably had already laid their eggs judging from the enlarged condition of their oviducts. Immature specimens of various sizes, seemingly representing at least two successive annual age-groups, were examined as follows: 43 mm snout-vent, October 12 (young of the year probably about a month old or a little more); 43 mm June 7 (first-year young hatched in previous summer); 60 mm August 1, one-year-old; 63 mm August 3, one-year-old; 74 mm May 4 (second-year individual after one full season of growth and two hibernations); 79 mm October 11 (second-year individual after one full season of growth and one hibernation). Possible third-year individuals were of the following sizes: 89 mm May 19; 89 mm August 17; 93 mm July 19;

100 mm August 9; 101 mm April 15; 101 mm June 4; 101 mm June 29; 102 mm August 9; 108 mm August 9; 109 mm August 7.

Farther south the growing season is longer, and breeding occurs earlier in spring. Ratios of nongravid to gravid females from southern California in spring and summer were as follows: in April, 1 to 4; in May, 1 to 4; in June, 1 to 6; in July, 1 to 0; in August, 2 to 0; in September, 1 to 0. Shaw (1943:194) reported finding a clutch of 20 eggs in a gopher burrow on June 1, 1942. All had hatched on July 25. Atsatt (1952:276) reported 12 eggs laid on June 8, 1941, which hatched August 16 and 17. Gander (1931:14) recorded a clutch of 15 laid on July 17. Stebbins (1958:25) stated that eggs laid in captivity had embryos at the limb bud stage.

Burrage (1965:512) stated, "Both wild and captive *G. m. nanus* and *webbi* lay 2 clutches of eggs per year and occasionally a third. Marked *nanus* and *webbi* females in the field that laid 2 clutches early in the season were found to be gravid again in September. Marked and unmarked gravid *webbi* females have been found in the field as early as 16 April, and as late as 24 September, and those of *nanus* from 24 April through 8 September. . . ."

In southern populations individuals attain larger average and maximum size, and the reproductive potential is higher, not only because of production of second clutches, but because clutches average larger. Egg counts for nine Oregon *G. m. scincicauda* averaged 9.0 (8 to 11). For 13 *G. m. multicarinatus*, from the Sacramento Valley and San Francisco Bay region, clutch size averaged 11.62 (6 to 17), and for 13 *webbi* from southern California, clutches averaged 11.83 (5 to 20). Burrage reported upon 25 clutches of *webbi* which averaged 13 (5 to 41) eggs, and 12 clutches of the insular *G. m. nanus* which averaged 10 (1 to 18) eggs.

Ophiodes

This is a South American genus in which the forelimbs are absent and the hind limbs, though present, are much reduced. According to Greer (1967:95) only *O. vertebralis* is known to be a live-bearer; he found 9 and 15 eggs in two gravid females. Two *O. intermedius* females each contained 11 oviducal eggs.

Ophisaurus

The several species of "glass snakes" are elongate legless lizards, occurring in Europe, Asia, and North America, in the Temperate Zone and also in the tropics. Insofar as known, all are oviparous. The female deposits eggs in a burrow and "guards" them throughout their incubation. Hence, one clutch per season is the rule.

Ophisaurus apodus.—Conant and Downs (1940:35) wrote that two eggs were found on July 20, 1937, in a cage with several female scheltopusiks received at the Philadelphia Zoo from the London Zoological Society.

Ophisaurus attenuatus.—Ecology of the slender glass lizard has been studied by me at The University of Kansas Natural History Reservation in the northwestern part of the range. In this area the lizards emerge from hibernation in late April or early May, and the breeding season is in the latter half of May.

Adult males are much more in evidence than are adult females in the breeding season. The eggs are normally deposited in June or July, as late as July 27 (Gloyd, 1928:119). The female remains with her clutch after ovipositing, and her presence may benefit the eggs, by turning them and by maintaining the humidity of the nest chamber. However, the female is not aggressive in defending the eggs against predators, and at times she may feed upon the eggs herself. During incubation the female's food consumption is slight, and she is sluggish and inactive and is losing weight. Hence, there is no possibility of the production of more than a single clutch in a season. Typical sizes for glass lizards of different ages are as follows:

hatchling	60 mm	snout-vent,	1 g
one-year-old	120 mm	snout-vent,	9 g
two-year-old	180 mm	snout-vent,	30 g
three-year-old	210 mm	snout-vent,	47 g

Breeding maturity is attained in the third year by some, but probably postponement until the fourth year is more typical. Hence, the population turnover is gradual as compared with that of most small lizards.

At the University of Kansas Natural History Reservation over a period of years the following records of clutches from females that laid their eggs in captivity or were dissected before laying, were gathered: 6, 7, 8, 8, 9, 10, 10, 16, 16, 16, 17. Also, two gravid females kept in the same container produced 20 eggs between them. Clutches of 8 (Gloyd, 1928:119) and 11 (Blair, 1961:201) have been reported in the literature. For the total of 15 clutches mentioned above, the average was 10.8 eggs.

Ophisaurus gracilis.—M. Smith (1935:394) wrote that in the eastern Himalayas this lizard produces four to seven eggs in July or August.

Ophisaurus hartii.—M. Smith (1935:394) cited Pope who found a female of this Chinese species in a nest guarding eggs on August 17. Hatching occurred in September.

Sauresia

This is a monotypic genus of Hispaniola. Greer (1967:96) found a single fetus that was almost full term in a gravid female of S. *sepsoides,* thus demonstrating that these lizards are viviparous.

Wetmorena

This is a monotypic Hispaniolan genus. Greer (1967:96) listed two gravid females of *W. haetiana* with three and eight eggs. In one there were almost full term embryos demonstrating viviparity.

Anniellidae

This family includes one genus of small, viviparous, legless lizards, *Anniella,* in California and Baja California. They burrow in sandy places. According to Miller (1944:274) *A. pulchra* ovulates in late May and early June. Females containing embryos have

been found on August 31, September 15, November 10, November 11; Stebbins (1954:304) recorded births on October 8 and 15 and stated that young (one to four, but most often two per female) are born in September, October, or November. As much as three years may be required to attain maturity.

Xenosauridae

This family has only one genus, with three localized species, in Mexico and Guatemala; (the genus, *Shinisaurus*, in China is sometimes included also or sometimes allocated in a separate family, the Shinisauridae). These lizards are viviparous. Fritts (1966:598) discussed the reproduction of *Xenosaurus grandis* on the basis of information gleaned from several preserved specimens. Four females from Veracruz, Mexico, collected January 3 and January 16, 1939, contained preovulatory eggs nine to 12 mm in diameter. Three other females collected at the same locality on July 9, 1964, all contained embryos in an advanced stage of development. Eggs or embryos numbered four, five, and six each in two females, and seven in one, for an average litter of 5.2. Alvarez del Toro (1960: 128) wrote that in Chiapas, Mexico, *X. grandis rackhami* produces a litter of three young and the time of birth is from March to July.

Helodermatidae

These large oviparous lizards inhabit arid regions in western México and the southwestern United States. Bogert and Martin del Campo (1956:120) suggested a two-year breeding cycle in the Gila monster, *Heloderma suspectum*, since a captive female that did not produce one year became gravid the next. Gates (1956: 184) kept a pair in captivity and observed copulation on June 4, 1955, and again on June 9 and September 30. The female died on November 12 and was found to contain five eggs 26.8 × 14 mm. A female from near Yuma, Arizona, laid six eggs during the first three weeks of July (Funk, 1966:255). Curtis (1949a:148) received a female Mexican beaded lizard, *H. horridum*, on October 14, 1948, and she laid a clutch of 15 eggs over a three-week period from January 31 to February 20. In Chiapas, Alvarez del Toro (1960: 122) noted that the female of this species lays a clutch of four to eight eggs from October to December. Taub (1963:149) stated that a female of *H. horridum* which had lived for 20 years in a zoo died in July 1961 and was found to have three eggs in each oviduct.

Snakes

Boidae

This primitive, widely distributed family is here construed to include the pythons, which, however, differ from the typical boas in reproductive habits and in various anatomical characters. Pythons have often been ranked as a distinct family, or at least subfamily; they are oviparous, whereas typical boas are viviparous. In the pythons clutches of eggs are usually large, and the female coils around them and guards them until the time of hatching, except as she may leave temporarily to feed, drink, or shed. Pope (1961:141) noted that effective concealment of the many large eggs would be difficult, and that a big snake is an effective protector for them. Nevertheless, descriptions of the behavior of brooding pythons in nature and in confinement, indicate that they are not especially aggressive at this time, but rather tend to be lethargic. Pythons guarding their eggs in zoos have often been studied and much evidence has accumulated to indicate that several of the giant species, coiled in a compact mass about the clutch, are able to raise their own body temperatures and those of the eggs above environmental temperatures, thereby hastening development. Substrate temperature exerts far more influence than air temperature on the snake's temperature, and failure to recognize this prevented definitive conclusions in all early studies of incubation, where the air temperature received most attention. Seemingly the incubating Indian python is unique in that at rather regular intervals the body undergoes shivering muscular contractions by means of which she maintains her temperature at a relatively high level when her surroundings are cool.

Boa

These large Neotropical boas are normally viviparous, but a remarkable incident cited below demonstrates that occasionally at least they can still produce shelled eggs. In Chiapas, México, Alvarez del Toro (1960:148) stated there were from 20 to 50 young at a birth in *B. constrictor*. Pope (1961:137), on the basis of published records, gave the number of young in a litter as 21 to 64. Hoover (1936:62) received a female from Central America in May, 1934, and on July 19 she gave birth to two fully developed young and also laid 13 leathery shelled eggs. Stuart (1948:62) mentioned a female in Alta Verapaz, Guatemala, which in early April contained 11 well developed eggs. In British Honduras, Neill (1962:241) obtained two gravid females, each about six feet long. One gave birth to 16 young on August 10 and the other to 12

young on August 19. Mole (1924:239) stated that on Trinidad the breeding season included December, January, February, and March, and he mentioned young born in May.

Charina

This monotypic genus includes only the rubber snake, a blunt-tailed dwarf boid of secretive and somewhat fossorial habits, in the western United States and adjacent Canada in relatively cool climates, mainly in or near coniferous forests. Like other boas the rubber snake, *C. bottae*, is viviparous. Tanner and Tanner (1939:28) wrote that in Utah young are normally born in September, but speculated that some births might be delayed until early spring. Svihla (1943:128) wrote that a female captured in Washington produced a litter on September 20 or 21. Erwin (1964:222) observed birth of young on August 24, to a Californian female. Litters of young born in captivity, or embryos in gravid females, numbered as follows: 2, 3, 3, 4, 4, 5, 6, 8, average 4.4 (Fitch, 1936:644; Svihla, 1943:128; Stebbins, 1954:354; Wright and Wright, 1957:55, 59).

Corallus

These are medium-large arboreal Neotropical boids. Mole (1924:237) mentioned a pair of *C. enydris* captured while mating in February in Trinidad. The female of this pair gave birth to between 20 and 30 young the following August. A large female of *C. caninus* in the American Museum of Natural History that died after 40 days of captivity, contained ten seemingly full term fetuses on November 14, 1927.

Epicrates

This is a genus of medium to large Neotropical boas, with representatives in the West Indies and in Central and South America.

Epicrates cenchria.—Mole (1924:236) mentioned mating observed in Trinidad in October and January. The female involved in the first observation gave birth to a brood in July.

Epicrates striatus.—Hanlon (1964:143) observed reproductive activities in Bahaman boas in captivity. One captured on June 19, 1960, gave birth to 51 young on September 19. In 1962 courting was observed on March 13 and copulation was noted on March 14, April 3, April 8, and April 13. One copulation lasted from 7:45 p.m. on March 14 until 8 a.m. on the following day. There were two males and three females in the group, and each mating involved a different combination of individuals. On October 17, 12 young were born to the female that mated on March 14 and April 8.

Eryx

Sand boas are small, burrowing snakes that occur chiefly in desert regions of southeastern Europe, Asia, and Africa.

Eryx colubrinus.—Loveridge (1936:234) reported that in East Africa on April 24, 1934, a native brought in a female and seven young, evidently her recently born litter; all eight snakes were found together in a burrow.

Eryx conicus.—Minton (1966:120) reported that in West Pakistan a female 670 mm long gave birth to a single young on July 11, and another female 710 mm long gave birth to 11 young on July 21.

Eryx jaculus.—Fuhn and Vancea (1961:271) stated that in Romania this dwarf sand boa lays six to 12 eggs in July, and the eggs hatch immediately.

Eunectes

The giant South American anaconda is partly aquatic. Pope (1961:137) stated that the number of young usually ranges from 28 to 42 in *E. murinus.* He mentioned broods of 19, 28, 30, and 72, the latter number said to be the young of a 19-foot female. Neill and Allen (1962:73) stated that an anaconda captured in British Guiana in October, 1958, gave birth to four young on the following January 8 and 9, and also extruded abortive eggs. The latter, along with fetal membranes, were devoured by the parturient female. On the basis of observations made in Trinidad Mole (1924:238) stated that mating occurs in December and January, and that the young, numbering 32 to 40 per litter, are born in July or August. Bellnomini and Hoge (1958:187) mentioned a litter of 82 young removed from a female by Caesarean section. Eight of these young survived.

Lichanura

These are medium-small boas of chaparral and desert habitats in the southwestern United States and adjacent México. Wright and Wright (1957:64) stated that there are usually 6 to 10 young, born alive, in *L. roseofusca.* They recorded a female from Sonora, México, that contained three embryos, and another that on June 29 had two embryos estimated to have completed about two-thirds of their development. Klauber (1933:214) mentioned a litter of six born November 16. Kurfess (1967:478) observed mating in captives on June 17, soon after the male was introduced into the female's cage. Five young were born on October 26 after a presumed gestation of 131 days.

Liasis

These are large to giant pythons of the Australasian region. Pope (1961: 129) mentioned a record of a female *L. amethistinus* found coiled around a clutch of 19 eggs.

Python

Typical pythons are large or giant snakes, in Africa, southeast Asia, and the East Indies.

Python curtus.—Noble (1935:1) observed reproduction of the blood python in captivity. A female from Sumatra laid 16 eggs in January, 1934, and re-

mained coiled about them. A check of her body temperature on February 11 indicated that it was not above that of her surroundings. Schmidt and Inger (1957:181) mentioned a clutch of ten eggs.

Python molurus.—Wall (1921:65) wrote that mating of the Indian python occurs in December, January, and February; eggs are laid in March, April, May, and June. Smith (1943:109) wrote that in northern India the mating of this giant snake takes place in the colder part of the year. Pope (1961:123-146) summarized many records of breeding mostly based on individuals kept in zoos far from their natural habitats, as follows. In 16 clutches there were 15 to 54 (average 29) eggs and there are records, probably authentic, of clutches of 100 and 107 eggs. There is one record by Wall of a female killed on Ceylon and found to contain large eggs on August 2. Five successful incubations of clutches in captivity, ranged from 57 or 58 to 66 days. Pope mentioned individuals kept in captivity by Stemmler-Morath which bred annually for several years. A female hatched in 1945 bred in 1950. Several males copulated with her in the period April 22 through May 9 and she laid eggs on June 28. Dowling experimented with an incubating Indian python in the period April 24 to May 17. During this time her surroundings varied from 78° to 90.5° F, but the snake kept her temperature within one degree of 90° F. The quivering muscular contractions with which she maintained her temperature were especially frequent when surroundings were cool, according to Pope.

Python regius.—Pope (1961:141) stated that this African python has been credited with laying eggs as well as giving birth.

Python reticulatus.—The reticulate python is Asiatic and is one of the largest living snakes, therefore much in demand in zoos, and best known from observations on captive individuals. Pope (1961:123-146) reported clutches of eggs laid by females of various lengths as follows: 10 feet—15 eggs; 10 feet—16 eggs; 11½ feet—14 eggs; 13½ feet—34 eggs; 18 feet—about 50 eggs; 18 feet—33 eggs; 20½ feet—57 eggs; 23 to 26 feet—103 eggs; about 26 feet—96 eggs. Dates of laying in captivity were in the months April through October. Incubation lasted 80 days in two instances and 55 to 60 days in one. In this species as in other pythons the eggs already contain small but well formed embryos at the time of laying. Unlike Indian pythons, females of this species that bred in captivity, seemed incapable of producing a clutch annually.

Python sebae.—The African rock python is another of the largest living snakes. Broadley (1959:11) wrote of a female found in southern Rhodesia with 39 eggs and hatchlings on December 24, 1956. One was recorded on Damba Island, Angola, with 50 newly laid eggs at the end of January. A 14-foot female was found containing eggs ready to be laid in Natal on June 2. In captivity one laid on January 12 and another on April 5. Pope (1961) stated the average clutch was 46 eggs and mentioned individual clutches as follows: 20, 23, 23, 26, 29, 31, 34, 38, 40, 44, 49, about 50, 51, 54, 55, 57, 58, 62, 69, "about 100." Pope, in describing Dowling's experiments with incubating pythons, stated that a rock python kept from 2½ to 4 degrees warmer than its surroundings (substrate 81° F) did not undergo quivering such as occurred in an Indian python. At 77° to 93° a clutch required almost 100 days of incubation.

Trachyboa

These are small Neotropical boas. Barbour (1937:139) received a female, probably *T. boulengeri,* from Panamá in April 1936, which contained embryos four inches long; he estimated that they would have grown another inch before birth.

Typhlopidae

This family contains small fossorial snakes of wormlike appearance, and having vestigial eyes. The family is pantropical in distribution, occuring even on remote Pacific islands and extending into the warmer parts of the temperate zones. Oviparity is the rule but there is at least one record of viviparity.

Typhlops

This large genus of blind snakes, with more than 160 recognized species, has a distribution comparable with that of the family. The number of eggs seems to vary greatly among different species.

Typhlops avakubae.—Bogert (1940:16) mentioned a female found in a termite nest at Kassa, French Congo, on October 25, 1930, with three newly hatched young and three eggs still unhatched.

Typhlops bibroni.—FitzSimons (1962:69) stated that in this South African species there are from five to eight eggs per clutch. Bogert (1940:15) mentioned a female from Natal that contained five eggs in December 1932.

Typhlops blanfordi.—Loveridge (1942:255) mentioned a female from Mushogero, East Africa that contained nine oviducal eggs on February 3.

Typhlops braminus.—In the Loo Choo Islands of southern Japan, egg-laying extends from June to September according to Fukada (1965:73). He cited an instance of two eggs laid on August 9, 1912, and stated that there are usually three to six eggs. Wall (1918:380) mentioned eight gravid females from Assam over the period from April to July. Cagle (1946c:101) reported that a gravid female collected on the Pacific island of Tinian deposited three eggs on April 21 (two days after capture). Two of the eggs hatched on May 29. In West Pakistan, Minton (1966:115) reported gravid females in December, January, and early May, and hatchlings on August 3 and September 7.

Typhlops diardi.—Wall (1918:382) stated that the embryos are partly developed when the eggs are laid and that there are five to eight eggs per clutch. Smith (1943:44) stated: "A very large specimen of *T. diardi* . . . obtained by me near Saigon contains 14 embryos all perfectly developed." E. H. Taylor (pers. com.) suggests that "*T. diardi*" may consist of two or more species, differing in their reproduction.

Typhlops lumbriciformis.—Loveridge (1936:229) mentioned a female from Kenya that contained four oviducal eggs on June 29, 1934.

Typhlops punctatus.—Loveridge (1942:256) mentioned one female from East Africa containing 19 oviducal eggs on July 1 and another that had 10 eggs on July 12.

Typhlops schlegeli.—In southern Rhodesia, Broadley (1959:9) examined a gravid female that contained 37 eggs on May 31, 1957. FitzSimons (1962:74) stated that in southern Africa the eggs are as few as 12 in young adults to as many as 60 in old adults, and are laid with embryos already partly developed, in late spring and early summer. The eggs require from a month to six weeks to hatch.

Leptotyphlopidae

These small wormlike snakes are remarkably similar to typhlopids in external appearance, but are well set off from them by important structural differences. All are in the genus *Leptotyphlops,* which has about 40 species in Asia, tropical Africa, and the American tropics northward to the southwestern United States. A brooding colony of *L. dulcis* was found by Hibbard (1964:222) on the shortgrass plains of southwestern Kansas, in a bank at a depth of 2½ feet, beneath sandstone and a surface layer of silt. Altogether there were 42 eggs which seemingly comprised six clutches, and in most instances, if not all, a female was coiled around the clutch of eggs when they were found on July 10, 1962. Beneath some of the clutches were old, dry, open eggshells, which seemed to be those that had hatched in previous years. At another nearby site, on July 5, 1961, Hibbard had found four gravid females containing 4, 3, 3, and 2 eggs, within three feet of each other in a bank, about 18 inches beneath the surface and two feet back from the exposed soil of the cut bank.

In southern California Klauber (1940b:148) studied *L. humilis* and noted that most females were carrying eggs in early summer, and he assumed that egg-laying occurred in late summer. He recorded gravid females with egg-complements of 2, 2, 3, 4, 4, 6 and 6 eggs. Newly emerged young were found to be about one-third of the maximum length of adults. Alvarez del Toro (1960:145) reported that in Chiapas, southern Mexico females of *L. phenops* produce eight to 12 eggs, usually in June or July.

In southern Rhodesia, Broadley (1959:10) noted a female of *L. longicauda* having two eggs (21 × 4 mm) on November 22, 1957. Minton (1966:117) reported that a female of *L. blanfordi* captured in West Pakistan in early December contained a single elongate egg (25 × 2.5 mm).

Acrochordidae

The wart snakes are medium-sized to large, with bulky bodies, loose skins, granular scales and no ventral plates, as they are highly specialized for aquatic existence and helpless on land. Although these snakes have often been allocated as a colubrid subfamily, recent studies by Underwood (1967) have indicated that relationships are with the henophidians, including some of the most primitive groups of living snakes—boas, pythons, uropeltids and xenopeltids. The two species occur in the Old World tropics, mainly in coastal regions from southern India to northern Australia and the Philippines. Both are viviparous. Smith (1935:134) wrote that *Acrochordus javanicus* produces 25 to 32 young, and *A. granulatus* produces six to eight.

Uropeltidae

The seven genera are confined to India and Ceylon and are specialized for fossorial existence; the head is small, not distinct from neck and with skull bones solidly united. The tail is remarkably short and blunt, and is rough or spiny. According to Smith (1943:64) "As far as is known all the species are viviparous, producing 3 to 8 young at a time." The genus *Uropeltis* has more than 20 species, chiefly in southern India, with one species in Ceylon. In these snakes the blunt tail is cylindrical or obliquely truncate, the terminal scute ending in two points side by side, or a transverse ridge. Wall (1918:634) wrote concerning the ocellate thistle-tail, *U. ocellatus*: "I have lately ascertained that it is viviparous in habits. The season of birth apparently ends in July in the Nilgiris." He recorded that two females contained three and five fetuses.

Colubridae

This is the dominant family of living snakes. They are of cosmopolitan distribution except in climates too cold for reptiles to exist, and on remote oceanic islands. They have undergone an adaptive radiation to occupy a great variety of habitat types and have achieved specialized habits and morphology for such ways of life as terrestrial, fossorial, psammophilous, arboreal, aquatic, and even incipient marine, and for diets such as worms, slugs, centipedes, snails, fish, frogs, and mammals. There are some 270 living genera according to Schmidt and Inger (1957:187). Less than one-third of these genera are considered here but perhaps these con-

stitute a representative sample. Little or nothing is known concerning the reproduction of most of the remaining kinds.

Oviparity is the general rule among the colubrids, and there are few exceptions. Among the genera here considered, the rear-fanged *Ahaetulla* and *Psammodynastes* of the Old World, *Tachymenis* and its near relatives in South America and the aglyphous *Coronella, Duberria, Pseudaspis, Conopsis, Toluca, Meizodon, Helicops,* one species among the many of *Elaphe,* nine genera of North American natricines (plus the Asiatic *Natrix annularis*), and all of the homalopsine water snakes are the only known viviparous types.

There has been much difference of opinion as to the proper familial limits of the Colubridae. The Aerochordidae, here dealt with as a distinct family, have often been included, and the dipsadines and pareatines have often been considered a distinct family. Underwood (1967) suggested reassigning many of the genera traditionally placed in the Colubridae to the "Dipsadidae," "Homalopsidae" and "Natricidae."

For the purpose of the present paper, the natricines and the relatively small groups of genera comprising dipsadines, pareatines, xenodermines, sibynophiines, dasypeltines and xenodontines have each been discussed as subfamilies, and the remaining genera comprising the great majority have all been included in the large subfamily Colubrinae. Conforming to some degree with traditional lines of division, the colubrines are here discussed in two alphabetical series of genera, the aglyphous or harmless snakes, and the opisthoglyphous, or rear-fanged group.

Colubrinae

Aglyphous series

These nonvenomous snakes include a bewildering array of forms not readily subdivided into orderly suprageneric units. Nearly all the species are oviparous. Two of the exceptions, *Coronella austriaca* and *Elaphe rufodorsata,* have ranges extending farther north and into cooler climates than most other snakes, so that their viviparity is of obvious adaptational value. There is no such ready explanation for viviparity in the African slug-eaters *(Duberria),* although they do range into fairly cool climates in the South Temperate Zone. Of New World genera, seemingly only the aquatic Neotropical *Helicops* and the montane *Conopsis* and *Toluca* are viviparous.

Adelphicos

This is a Neotropical genus. Stuart (1948:78) wrote that in Alta Verapaz, Guatemala, the eggs of *A. varaepacis* are deposited just before the start of the rainy season in May.

Alsophis

These are slender, diurnal, terrestrial, oviparous, Neotropical snakes. Perkins (1943:110) received a pair of Cuban *A. angulifer* at the San Diego Zoo in April, 1939, and the female produced clutches of 9, 8, and 9 eggs in 1939, 1940 and 1941; egg-laying was on August 24, August 17 and July 19. Incubation took 95 days in 1939 and 89 to 94 days in 1940. Copulation was observed on May 28, 1940 and May 27, 1941.

These few records suggest that in the subtropical but somewhat seasonal climate of Cuba this endemic snake has a short breeding season and stereotyped breeding schedule resembling the schedules of various kinds of snakes in temperate North America. However, the interval between copulation and egg-laying is notably long, and recorded hatching dates are late in the fall in *Alsophis angulifer*.

Arizona

The glossy snakes comprise a single polytypic species *(Arizona elegans)* of nocturnal oviparous colubrines, in the southwestern United States and northern México. There are brief accounts of its reproduction by Burt and Hoyle (1934: 208), Reynolds (1943:196), Cowles and Bogert (1944:285), Klauber (1946: 378), and Wright and Wright (1957:91, 93, 95, 97, and 101). Clutches mentioned by these authors contained: 3, 4, 4, 5, 6, 7, 7, 9, 9, 10, 10, 10, 12, and 23 eggs—average 8.5. The clutch having 23 eggs was laid on July 8 and hatched after 68 days.

Aspidura

The rough-sides are a genus with five species of small, secretive oviparous snakes that feed upon soft-bodied invertebrates. They are confined to Ceylon and the Maldive Islands. Smith (1943:336) stated that two to five eggs at a time are laid by females of *A. brachyorrhus*. The same author (1943:337) cited a record of a female of *A. copii* that contained 21 eggs. Wall (1921:211) wrote that *A. trachyprocta* usually lays from four to 12 eggs, and that breeding seems to continue through most of the year. In series collected in February and March many of the females were gravid.

Atretium

The two species of keelbacks in this genus are found in Ceylon, India, and Yunnan and are oviparous. Wall (1921:130) recorded a pair of olivaceous keelbacks, *A. schistosum*, mating at Bangalore, India, on August 27. He reported egg-laying on April 26 and on January 1. A female was nearly ready to lay on December 9. A long breeding season is indicated. Smith (1943:320)

stated that from 12 to 30 eggs are laid, and Wall (1912:1014) mentioned clutches of 10, 18, and 20.

Boaedon

This genus of the African house snakes, is primarily tropical. The few records of breeding indicate a breeding season extending over much of the year and show that a female can produce successive clutches of eggs in a season.

Boaedon fuliginosus.—In southern Rhodesia, Broadley (1959:14) observed captives in copulation on September 16 and 17. A female (not the one seen mating) laid seven eggs on November 10. In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman and Chapman (1962:426) noted females containing developing ova in February, May and August. In May one contained 10 large ova. In September one had seven large oviducal eggs and also ovarian eggs six mm in diameter. FitzSimons (1962:122) stated that there are usually eight to ten eggs (up to 16) laid in spring or early summer.

Boaedon lineatus.—Loveridge (1936:239; 1942:264) published notes concerning the reproduction of this East African house snake. He recorded gravid females with oviducal eggs on the following dates: December 16, January 11, March 1 (two females), March 11, March 25, May 10, at Butadinga, Sipi, Kaimosi, Lamu Island and Ujiji. Numbers of eggs per clutch were: 1, 1, 2, 5, 6, 7, 8, and 10. Six eggs were found in a termite nest on February 2. Blackwell (1954:136) observed egg-laying in a captive female. She was received in November 1952; on January 30, 1953, she laid six eggs most of which were fertile. On April 16, 1953, she laid a second clutch of eight, but it was not determined whether these were fertile, because they were deposited in a water dish and soon spoiled.

Calamaria

These small, secretive and burrowing tropical colubrines occur in the Malayan region and the Indo-Australian Archipelago. Limited information is available regarding the reproduction of two species; seemingly breeding occurs year-round.

In western Java, DeHaas (1941:343, 348) found that in *C. lumbricoidea* the ratio of adults to young changed markedly during the course of the year. In February and May the catch consisted entirely of adults, but through the summer months immatures made up about half of the catch, rising to a maximum of 78 per cent in October, and then declining in winter. Seemingly there is year-round breeding, as gravid females were recorded in every month of the year. However, they were best represented in the period June through September; at other times of year the incidence of breeding is much reduced.

DeHaas obtained *C. linnaei* in even greater numbers than the preceding species. Adults were taken in relatively large numbers (70 to 90 per cent of catch) from June through October, then decreased to near 50 per cent through November, December, and January, and increased again abruptly in the late winter and spring. As in *C. lumbricoidea* gravid females were secured in every month. But in *C. linnaei* there is no season of concentrated reproductive

activity; the maximum numbers of gravid individuals were taken in March (13), June (12), and August (15) with month-to-month fluctuations such as might be expected if chance were the main determining factor.

Cemophora

The only species is the scarlet snake *C. coccinea* of the southeastern United States, a small secretive, burrowing, oviparous snake much like a milk snake in appearance. Carr (1940:86) recorded a female that contained eight large eggs on June 2. Wright and Wright (1957:115) recorded one clutch of three eggs, and another of eight, the latter laid on June 23. Woolcott (1959:263) wrote of five eggs found near Richmond, Virginia, on September 12, 1956; they hatched 13 days later. These few records indicate that the season of egg-laying is lengthy and suggest the possibility that females may produce more than one clutch in a season.

Carphophis

This genus contains the worm snakes, small, smooth-scaled oviparous colubrines corresponding well in overall distribution with the original deciduous forests of the eastern United States, in nonglaciated areas. They show strong fossorial adaptation. Donald R. Clark, Jr. made an ecological study of *C. vermis* at the University of Kansas Natural History Reservation and nearby areas in northeastern Kansas; he provided the following information from two seasons of field work on this local population. Mating occurs in September and October and perhaps also in spring. Ovulation occurs mainly between April 23 and May 5. Fifty counts of oviducal eggs (from palpation of live snakes) yielded an average of 3.14 (1 to 5) per clutch. For large ovarian eggs, counts were somewhat higher and for clutches actually laid in captivity they were somewhat less, indicating loss during development. Two clutches incubated indoors but at temperatures approximating those in the field, hatched in 48 and 49 days. Worm snakes mate when three years old, in fall, or perhaps early in the third year, in spring. In Kentucky Barbour (1960:10) found a somewhat smaller average clutch (2.6 eggs), with egg-laying occurring about mid-June, in *C. amoenus helenae*.

Coluber

The racers, fast-moving terrestrial colubrines of the North Temperate Zone, conform to a breeding schedule typical for snakes of that region, with copulation and egg-laying in spring, and hatching in late summer. There is no evidence of individuals producing more than one clutch per year. In *C. constrictor* there is notable geographic variation in size of clutch.

Coluber constrictor.—The common racer occurs over most of the United States. The breeding cycle is best known in northeastern Kansas, the center of the geographic range, where a 14-year field study (Fitch, 1963:459) showed that mating occurs chiefly in May and during that month the male is especially active in sexual search. Ovulation occurs most typically in late May but sometimes in June. The eggs are laid from mid-June to early August. In each

breeding season some females of adult size are not fecund. Approximately 13 per cent of the two-year-olds in a summer sample were productive, breeding for the first time, and the percentage of fecund females was greater in each successively older age group to a maximum of approximately 80 per cent in old adults. Two-year-olds averaged only 9.2 eggs per clutch, whereas those that were six years old or older averaged 15.7. Incubation averaged 51 (43 to 63) days.

Bodily size varies somewhat over the geographic range, and number of eggs per clutch also varies. In the northeastern *C. c. constrictor,* 14 clutches average 16.8, whereas in *C. c. flaviventris* of Kansas, 62 clutches average 11.6 and in *C. c. mormon* of the West Coast, 43 clutches average only 5.8.

Coluber jugularis.—In Romania, Fuhn and Vancea (1961:277) found that impregnation occurs in early May and that egg-laying occurs from late June to early August.

Coluber rhodorachis.—In Iran, Anderson (1963:465) recorded a female cliff racer having oviducal eggs 34 mm in length on June 27 and another having ovarian eggs nine mm in diameter on July 4. At Karachi in West Pakistan, Minton (1966:122) noted the smallest young in August and September.

Coluber ventromaculatus.—This is a species of northwestern India and neighboring regions. Wall (1914:41) recorded three gravid females in May (containing 3, 8, and 9 eggs) and stated that the young appear in August and September.

Conopsis

These small colubrines, limited to high altitudes in México are insofar as known, viviparous, thus differing from the closely related genera *Ficimia* and *Gyalopion,* generally found at lower altitudes. Duellman (1961:92) found a copulating pair of *Conopsis biserialis* at Capácuaro, Michoacán, México, on August 1, 1956. Greer (1966:371) examined a series of *C. nasus* collected at Alvarez, 7500 to 8000 feet, San Luis Potosí, México, in October and November. In 20 gravid females embryos averaged 3.6 (1 to 6).

Coronella

The European smooth snake *(C. austriaca)* resembles the North American king snakes *(Lampropeltis)* but is viviparous. Smith (1951:240) stated that mating occurs both in autumn and in spring. The young are usually born in the latter half of August or in early September. In 50 litters numbers of young ranged from four to 12 except for one which had 13. The female is usually sexually mature at an age of four years. In Romania, Fuhn and Vancea (1961: 293) found that impregnation of females occurs in April and May, and young are born at the end of August or in September.

Dendrelaphis

The bronze-backs are active, slender, elongate, diurnal tree snakes that occur from the Himalayas through southern Asia and to Australia. Smith (1943:240)

stated that from three to five elongate eggs are laid at a time and that embryos are already partly developed at the time of oviposition. Worrell (1964:102) wrote that in *D. punctulatus* in Australia, five to 12 eggs are laid in December and hatching occurs after about three months' incubation. Wall (1910:784) reported clutches of 6 and 7 eggs in the Indian bronze-back *(D. tristis).* Wall (1921:226) reported gravid females of this species in January, February, August, September and December, and instances of egg-laying in January and August. Obviously breeding occurs through much of the year or all of it.

Diadophis

The ring-necked snakes are small, secretive, and terrestrial, and occur throughout most of the United States and in adjacent Canada and México. Traditionally, the numerous forms have been grouped into three species, *D. punctatus* (eastern), *D. regalis* (southwestern) and *D. amabilis* (Pacific Coast), but all may be conspecific. Observations on reproductive cycles have been made chiefly on the eastern forms. Copulation occurs in both autumn and spring, egg-laying in early summer and hatching in late summer or early autumn. Insofar as known, one clutch per season per female is the rule but possibly some females produce second clutches. Females ordinarily mature and produce eggs late in the third year. Population studies in Michigan, Kansas and Florida have revealed differences in time of laying and numbers of eggs, as might be expected.

Diadophis punctatus.—Blanchard (1930, 1936) studied the eggs, nests, and young of the ring-necked snake in northern Michigan. There he found that oviposition is typically in the latter part of June or the beginning of July. For 202 clutches the average number was 3.5. There were seven eggs in just one clutch, 6 in 10, 5 in 27, 4 in 57, 3 in 64, 2 in 37, and 1 in 6. In general, number of eggs per clutch showed a good correlation with size (and presumably age) of the female. The smaller fecund females (310 to 360 mm in total length) usually had one to three eggs, those from 360 to 440 most often had three or four eggs, and the largest, over 440 mm often had five or six eggs. A typical incubation period was approximately 56 days.

In northeastern Kansas I found egg-laying to be concentrated in the last week of June and the first week of July. In a random sample of 49 clutches the number of eggs averaged 4.2 (1 to 8), with three-egg, four-egg and five-egg clutches occurring in almost equal frequency, and, in combination, making up three-fourths of the sample (Fig. 8). The number of eggs was found to be closely correlated with size of the female. The fecund females ranged from 226 to 379 mm in snout-vent length (267 to 443 mm total length). Eggs incubated in the laboratory generally hatched in early September. Probably the females do not breed until the third year, at an age of about 31 months.

Near the southern extreme of the range, in Florida, Myers (1965:43, 75-80) found that eggs are probably laid from late May or June into August and that females normally breed each year. Both sexes were thought to be sexually mature by their second spring. In 20 adults containing large ova the average clutch was 5.2 (ranging from 2 to 10, with 4 being the most frequent number). Myers' finding that egg-laying in Florida extends into August, later than in northern states, is of significance in connection with the possible production of second clutches in the prolonged growing season of the southern states. A

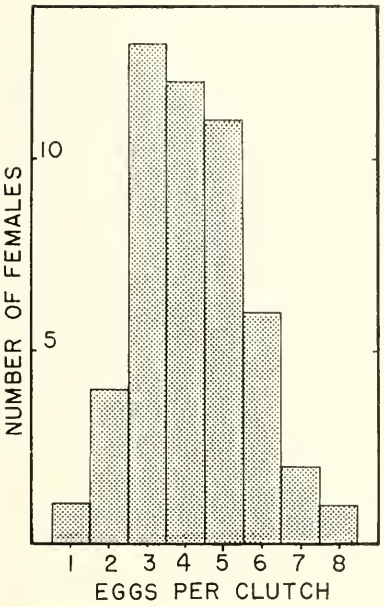


Fig. 8. Numbers of eggs per clutch in ring-necked snakes *(Diadophis punctatus)* from northeastern Kansas. In this sample of 49 females numbers of eggs ranged from one to eight, but most had three, four or five eggs. In 10 small females (226 to 253 mm snout-vent) perhaps all producing their first clutches, there were two to four eggs, average 2.4, whereas in 20 large females (311 to 379 mm snout-vent) there were two to eight eggs, average 5.4.

record published by Peterson (1956:152) of a female from Miami that gave birth to six young on May 21, 1955, is especially noteworthy not only as an instance of viviparity in this normally oviparous snake, but for the extremely early date of appearance of young, indicating departure from the usual breeding schedule in the subtropical climate at the southern extreme of the range.

Dinodon

This is an Oriental genus of oviparous terrestrial and nocturnal snakes. For *Dinodon orientale,* Fukada (1963:8; 1965:90) mentioned clutches of 2, 2, and 9 eggs. A female kept by him oviposited in July and the eggs hatched after an incubation period of 45 days. Pope (1935:206) mentioned two gravid females of *Dinodon rufozonatum* from the Tsinan region of China. One contained 11 eggs, the other contained "8 well-formed and 3 poorly developed ones." Fukada (1965:70) mentioned a female of *Dinodon semicarinatus* 902 mm in length that contained four oviducal eggs in July. This is a relatively large species of the Ryukyu Islands. The four species of the genus are slender-bodied, banded, Oriental snakes that are generalized feeders, preying upon common species of lizards, upon frogs, toads and freshwater fishes, and occasionally upon other snakes and small mammals. Pope (1935:206) commented upon the scarcity of breeding records for these relatively common snakes.

Drymarchon

These are large and bulky terrestrial oviparous colubrines, ranging from the southeastern United States to tropical South America. Recorded dates of

reproductive events for *D. corais* suggest conformity to a typical Temperate Zone schedule, except that all egg-laying dates are notably early. Groves (1960: 51) had a pair of Florida indigo snakes *(D. c. couperi)* which mated on October 30, October 31 and January 20. The female laid 11 eggs on the following May 6 and these hatched on August 7. Another female laid 6 eggs on May 28 and they hatched on September 10. A third female laid 9 eggs on May 14, 1956, and another clutch of 11 eggs on May 25, 1957. LeBuff (1953:166) recorded that a female captured on April 13 laid 6 eggs on May 2. A record of outstanding significance was that of Carson (1945:225) who purchased a female of this species from a dealer. After four years and four months in solitary confinement, this snake, on May 29, 1945, produced a clutch of five eggs, at least one of which was fertile. Wright and Wright (1957:206) observed captive individuals of *D. c. erebennus* at Brownsville, Texas, in late April, 1925: "Found 3 or 4 large eggs with some of them. They were dirty white, tough, rough eggs easily 4 inches long." Stuart (1948:67) wrote that a female *D. c. melanurus* in Alta Verapaz, Guatemala contained "partly formed eggs" in early June.

Drymobius

These racerlike Neotropical snakes extend northward to extreme southern Texas. The few available dates indicate egg-laying in spring.

Drymobius chloroticus.—In Alta Verapaz, Guatemala, Stuart (1948:64) found that females contained well-developed eggs in May.

Drymobius margaritiferus.—Gaige, Hartweg and Stuart (1937:18) reported a gravid female in August, and another that laid seven eggs on April 22. Two of the latter hatched on June 9 and 11. Werler (1949:59) reported that a female laid seven eggs on April 22 and two hatched on June 9 and 11. The same author reported a clutch of two eggs laid on July 29. In the Cayo District of British Honduras, Neill (1962:240) reported one 359 mm in total length on October 15, still retaining a faint umbilical scar, and probably only a few weeks old.

Drymoluber

These are slender and active Neotropical oviparous colubrines. *D. dichrous* in tropical rain forest seemingly has an extended breeding season, thus resembling most or all of the other snakes found in this same climate and type of habitat. A series of this species in the Bassler Collection of the American Museum of Natural History, from Iquitos, Perú, were examined by me. The two gravid females for which definite dates were available were collected in August. Three undated females also were gravid. Females contained 2, 3, 4, 5 and 6 ova, average 4.0.

Among the snakes examined were eight young that probably were not much beyond hatching size—227 to 273 mm in snout-vent length—and for these seasonal distribution was as follows: two in February, one in March, one in August, one in September, two in October, and one in December. On this somewhat meager evidence it is tentatively concluded that in *Drymoluber dichrous* as in the other common snakes of the Iquitos region, breeding is more or less continuous throughout the year.

Duberria

These small viviparous African snakes range from the tropics into the South Temperate Zone. Bogert (1940:40) recorded females of *D. lutrix* from the Rungwe Mountains in Tanganyika, which contained complements of 6, 7, 10, 10 and 17 eggs. Loveridge (1942:281; 1953:264) mentioned other gravid females of *D. lutrix* from East Africa on January 27 (four), early July, and November 8. They contained 7, 8, 10, 11 and 14 eggs. Broadley (1959:32) mentioned a female in southern Rhodesia which gave birth to seven young on December 27, 1956. FitzSimons (1962:169) stated that in southern Africa young may be born as early as October but are usually born in February.

Eirenis

These are small burrowing, desert snakes of southwestern Asia and northern Africa. Anderson (1963:467) reported finding of gravid females of *E. persica* in Iran on May 25 and August 30, 1958. One that was opened contained a single elongate egg.

Elaphe

The rat snakes comprise a genus of medium to large colubrines in Europe, Asia and North America, chiefly north of the tropics, and especially in forested areas of eastern Asia and eastern United States. Comparison of the data for the different species reveal some surprising contrasts. Oviparity is the rule, but one Asiatic species, *E. rufidorsata* is viviparous. The group as a whole conforms to the usual reproductive cycle of snakes in the Temperate Zone, with a spring breeding season, and emergence of hatchlings in late summer or autumn. There is notable difference among the species in length of time required from hatching to breeding maturity—less than two years in *E. quadrivirgata* and *E. guttata* (in captivity) to four years in *E. obsoleta*.

Elaphe carinata.—Pope (1929:438) described a nest of this montane Oriental species, in the high bamboo forest near Kuatun, China. A clutch of 12 eggs were found on July 29, in the loose decaying vegetation of a pile of bamboo waste. Hiding in the same pile of waste which contained the nest were three adult *E. carinata,* one of which was a gravid female containing 12 eggs.

Elaphe climacophora.—This large Japanese species is fairly well known through the studies of Fukada (1965:69). Mating is in May or June and egg-laying is from mid-July to early August. The female remains with the eggs, coiled around them, for several days after laying. In 18 clutches the number of eggs averaged 9.2. The known range is from 4 to 24, with only four or five produced by the smallest mature females and relatively large clutches produced by those in the larger size classes. Recorded incubation periods range from 51 to 64 days and average approximately 58.

Elaphe conspicillata.—This is another Japanese species smaller than the preceding, and more subterranean in habits. Fukada stated that mating occurs in May and June and egg-laying in July and early August. The female does not remain with the eggs. Eggs average four per clutch (1 to 7), and incubation requires approximately 50 days.

Elaphe dione.—Pope (1935:243) published several records of breeding in northern China, and he also cited earlier published records. Gravid females containing 4, 8, 8, and 11 eggs were reported in May and July and a clutch of 11 eggs was collected on July 18. Hatching of the latter occurred on July 27 and 28 and six hatchlings each with an egg-tooth were brought in on August 14-15. According to one statement (Sowerby, 1914:164) the incubation period is about three weeks. Webb, Jones and Byers (1962:167) noted that a female from Korea collected June 13 contained nine oviducal eggs.

Elaphe guttata.—Because the corn snake is common in the eastern United States, and thrives in captivity, its reproduction has been observed more often than that of most other snakes. Bechtel and Bechtel (1958:148-149 and 1962: 436-437) kept and reared corn snakes through several generations and were successful in breeding an albino strain from an original male that came from North Carolina. One surprising outcome of their work was the finding that in both sexes, sexual maturity is attained at an age of approximately 18 months, and that the females reared in captivity consistently laid their first clutches of eggs at an age of two years. However, it seems that these captive-bred snakes were not subjected to the same schedule of hibernation that they would have had in nature, and perhaps their development was accelerated by a prolonged season of activity and feeding. Records of their courtship and mating in January and March suggest that they were maintained at high temperatures permitting them to remain active throughout the year.

The published records of breeding, indicating periods of "gestation" and incubation are summarized in Table 6. Most of the records by Bechtel and Bechtel are of clutches laid by newly matured two-year-old females, and hence are relatively small. For the 17 clutches listed in Table 6, the average is 9.8 eggs.

Elaphe helenae.—In the Deccan of northern India, Lindberg (1932:695) found females containing eggs in July. In the Nilgiri Hills of southern India, Wall (1921:200) found no gravid females in a collection of 107 specimens in the months June to September, but a hatchling was taken on March 29.

Elaphe longissima.—Fuhn and Vancea (1961:290) stated that in the aesculapian snake in Romania impregnation occurs in May or June, egg-laying about a month later, and hatching in September.

Elaphe obsoleta.—The common rat snake occurs over much of the eastern half of the United States, and is subject to much geographic variation within this extensive area. Doubtless reproductive cycles vary in response to climatic and other environmental factors, but the extent of the change from one part of the range to another is poorly known. In northeastern Kansas near the northwestern limit of the range I made a 15-year study of a local population. Females generally produce their first clutches of eggs late in the fourth year of life when a snout-vent length of more than 870 mm has been attained. Copulation sometimes occurs in the autumn but mating activity is most often observed in late April and May. Egg-laying occurs in late June or July and hatching is from late August to early October. Wright and Wright (1957) summarized the literature. They reported clutches with the following numbers of eggs: 5, 6, 7, 8, 9, 10, 11, 12, 13, 14, 15, 16, 17, 19, 21, 22, 24, 44. Several clutches each with eight to 12 eggs were recorded, and seemingly the mode falls within this

Table 6. Reproduction in *Elaphe guttata*.

Authority	Origin of snakes	Date of copulation	Date of laying	Number of eggs	Date of hatching
Bechtel and Bechtel, 1958	Not recorded	April 4	May 30	8	August 13
Bechtel and Bechtel, 1958	Not recorded	March 18 and 19	May 11	6	----------
Bechtel and Bechtel, 1958	Not recorded	----------	May 19	5	----------
Bechtel and Bechtel, 1958	Not recorded	March 19 and April 4	May 26	3	August 7 to 9
Bechtel and Bechtel, 1962	Not recorded	January	March 28	21	June 13
Bechtel and Bechtel, 1962	Not recorded	January	April 6	17	June 25
Bechtel and Bechtel, 1962	Not recorded	January	April 24	13	July 11
Bechtel and Bechtel, 1962	Not recorded	?	June 6	11	August 31
Bechtel and Bechtel, 1962	Not recorded	?	June 17	7	September 9
Bechtel and Bechtel, 1962	Not recorded	?	June 13	8	September 18
Holman, 1960:239	Florida	May 24 and 27	June 26	----	August 28
MacMahon, 1957:232	Florida	May 26 and 27	July 2	11	August 29
Clark, 1953:90	Kansas	?	July 4	5	----------
Clark, 1953:90	Kansas	?	July 8	4	----------
Perkins, 1943:110	Texas	?	July 8 and 9	14	September 18
Werler, 1951:41	Texas	?	June 14 and 15	15	August 7 to 12
Parker, 1948:26	Tennessee	?	----------	18	----------

relatively narrow range. Wright and Wright cited the following dates of laying: June 11 (Texas), June 13 (Texas), June 16 (two clutches, Florida), June 24 (Texas), June 24 (Pennsylvania), July 2, 5, 11, 16, 17, 20, 21, 26, 26, 30, and August 6, 9, and 17. These last three records are from the southern part of the range, in Florida, Louisiana and Georgia, respectively, where reproduction is known to begin early in the season. In this part of the range oviposition in late

July and August probably indicates production of second clutches. Some recorded incubation periods for clutches in different parts of the range are: 53, 53 to 56, 59, 65, 106 and 109 days. Presumably the wide range in span of incubation periods is due to differences in temperatures at which the eggs developed, but perhaps the amount of embryonic development that takes place before laying is also subject to some variation. Slack (1944:190) recorded an 18-day interval between copulation and egg-laying in a captive female. Lynch (1966:305) reported the finding of 76 eggs in a single cluster, in Brown County, Indiana. These eggs might have been the combined clutches of only two giant-sized females that were killed in the vicinity the following year, but more probably they represented the combined clutches of several females. Old eggshells remaining from earlier years were also present at the nest site.

Elaphe quadrivirgata.—Fukada (1960:6-21) studied the life history of this Japanese species and found that snakes of both sexes mature late in their second year. The young hatch late in the season and grow little before the first hibernation; most of their growth is in the next full growing season, after their emergence from hibernation. Early in the third growing season (soon after emergence from the second hibernation) at an age of one year and nine months, the young are ready to breed. Hence, at the minimum, only two years per generation is required. The mating season is from late April to mid-June and egg-laying is from mid-July to early August. The female remains coiled around the eggs for several days after laying. In 56 clutches eggs averaged 8.9 (4 to 15). Size of clutch was correlated with size of the female. The smallest productive females, 90 to 99 cm in length laid an average clutch of 7.3 eggs (4 to 10), whereas the largest females, 130 to 139 cm, laid an average of 11.5 eggs (6 to 15). The incubation period is 40 to 57 days.

Elaphe quatuorlineata.—Fuhn and Vancea (1961:283) noted that in Romania impregnation occurs in June and July, oviposition in July, and hatching in September or October.

Elaphe radiata.—This is a common species of southeastern Asia. It is "apparently oviparous," according to Pope (1935:263), who cited a statement by Wall that females are to be found containing eggs in April, May, June, and July, and that the eggs number five to 12.

Elaphe rufodorsata.—This northern semiaquatic species of Korea, Manchuria, northern China, and adjacent parts of the U.S.S.R. is especially remarkable in being viviparous. Pope (1935:265) cited a statement by Sowerby regarding birth of "eight or ten" young and he himself recorded birth of litters on September 25. He recorded the following counts of eggs or embryos: 4, 7, 10, 11, 12, 12, 14, 16, 16, and 21. Maslin (1950:451) reported four gravid females from Kiangsi, China, which contained 10 to 16 eggs in which embryos were still not evident on June 7. Webb, Jones and Byers (1962:168) recorded copulation of a pair in Korea on April 25.

Elaphe schrenckii.—This is a species of northern China. Pope (1935:270) cited a Russian author (Emelianov), who stated that eggs in a clutch range from 13 to 30, that these are laid from mid-July to mid-August, and that the young emerge in late August or September.

Elaphe taeniurus.—This is a large and common Chinese species. Pope (1935:275) reported females containing 11, 12, 12, and 13 eggs, which were judged almost ready to be laid on June 28 and July 8.

Elaphe vulpina.—The fox snake is a relatively small species of the north-central United States. Wright and Wright (1957:264) reported clutches of 7, 9, 10, 11, 13, 14, 15, 17, 20, 21, and 29 eggs, average 15.1. They reported laying on June 14 and 24, July 17, 17, 19, 20, 21, 23, 29, and on August 5 to 6; hatching was recorded on September 18 to 20 and October 19.

Elapoides

These small terrestrial colubrines occur in the Indonesian region. In west Java, DeHaas (1941:343) found the largest numbers of gravid females of *E. fuscus* in the dry season when rainfall averaged 44 to 128 mm per month (May—17, June—18, July—19, August—14, September—33) but during the remainder of the year, with rainfall of 353 to 522 mm per month, he obtained fewer gravid females (October—4, November—5, December—10, January—8, February—3, March—11, April—10). Adults made up about 60 per cent of the June and July samples but from November through May immatures made up about 60 per cent of each monthly sample.

Farancia

This genus includes two prolific oviparous species in the southeastern United States. Insofar as known, one clutch per season is the rule, but the span of several weeks in dates of recorded oviposition raises the possibility that a female may produce more than one clutch per season.

Farancia abacura.—The mud snake is a large somewhat fossorial species. Meade (1937:12) observed copulation in caged individuals on July 11; eggs were laid on September 5 and hatching took place on October 30. Several observers have found females guarding their clutches of eggs or have noted that they have remained with eggs laid in captivity. Riemer (1957:31) reported a female in a burrow with her clutch, which was in process of hatching, near Gainesville, Florida, on September 19, 1956. Van Hyning (1931:59), Meade (1935:190; 1937:12), Carr (1940:78), Conant and Downs (1940:35), Reynolds and Solberg (1942:25), Wright and Wright (1957:274, 278), and Kennedy (1959:71) published statements regarding egg-laying. Recorded clutches of eggs found in nature, laid in captivity, or observed in gravid females number as follows: 4, 11, 15, 15, 16, 18, 20, 22, 24, 25, 25, 28, 28, 29, 35, 36, 40, 43, 48, 50, 50, 54, and 104, average 32.2.

Farancia erytrogramma.—The rainbow snake is a fossorial and partly aquatic species of the Atlantic and Gulf coasts from Maryland to Louisiana. In Virginia, Richmond (1945:30) found several nests in a sandy field. He found a gravid female on June 24 which contained shelled eggs not quite ready to be laid. On July 5 he found a female in the act of laying and on the same day found two other nests with eggs containing embryos 60 mm long. Ditmars (1936:284) reported a clutch of eggs laid on July 7. Clutches of 20, 22, 22, 33, 43, 47, 50, and 52 eggs, average 36.1, have been recorded (Wright and

Wright, 1957:85; Neill, 1964a:279). The latter author reported egg-laying in a captive female on July 8 and 9 and in another on July 10, and the finding of a natural nest on July 22.

Geophis

These are small, secretive, smooth-scaled, stubby-bodied colubrines. Numerous species occur in Mexico and Central America; some are montane. In the second week of February 1965, I obtained three gravid females of *G. brachycephalus* on Volcan Barba, Costa Rica. In the last week of March I obtained two nongravid females and three young of hatchling size between Volcan Barba and Volcan Poas.

Gongylosoma

Snakes of this genus are small, terrestrial and oviparous and inhabit the Indonesian region. In western Java, DeHaas (1941:346) found only adults of *G. baliodeira* in June at the end of the rainy season, but the number of young increased rapidly through July, August, and September (the dry season) and young were in the majority through October, November, and December, with a corresponding decrease from January to May. Bergman (1963:7) examined 19 egg-bearing females from Java that were 245 to 314 mm in body length. The average clutch was 2.5; one had 1 egg, 19 had 2 and 20 had 3.

Grayia

These tropical African aquatic, fish-eating snakes are oviparous. Angel, Guibé, La Motte, and Roy (1954:394) reported that a large female of *G. smithi* from Mt. Nimba in French Guinea contained 23 large eggs in May.

Lampropeltis

The genus is primarily North American, but one species ranges southward into northwestern South America. All species are oviparous; mating is in spring, egg-laying in early summer, and hatching in late summer in all recorded instances.

Lampropeltis calligaster.—Clutches of six to 17 (average 11.0) have been mentioned in the literature by Blanchard (1921:121), Shoop (1957:48), Minton (1944:463), Guidry (1953:50), Clarke (1954:15), Carpenter (1958:115), Dietrich (1960:47), Smith (1961:214) and Anderson (1965:240). Some dates of egg-laying are: June 19, 22, 23, 27, and July 1, 5, 13, 20 and 22. Shoop recorded clutches laid on June 19 and 27 which hatched on August 3 and 13 respectively. Anderson (1965:240) mentioned a clutch laid on June 23 which hatched September 3 to 5.

Lampropeltis getulus.—The "common" king snake occurs in the southern half of the United States. Wright and Bishop (1915), Cloyd (1928:127), Force (1930:32), Klauber (1939b:4), Van Hyning (1931:59), Blanchard (1921:53, 54), Conant (1934:66), Meade (1932:70), Boyer and Heinze (1934:196), McCauley (1945:91), Carpenter (1958:115), Brimley (1903:

264), Knepton (1951:85), Wright and Wright (1957:374, 380, 383, 385, 390, 393), Cunningham (1959:18) and Anderson (1965:245) reported clutches of eggs as follows: 5, 6, 6, 7, 7, 7, 8, 9, 9, 9, 9, 9, 10, 10, 12, 12, 14, 14, 16, 16, and 17, average 10.1. Mating has been reported on April 19 (Florida), May 14 (California), May 18 (Maryland), May 19 (Georgia), May 22 (California) and June 21 (California). Meade reported an instance of copulation in May, with egg-laying occurring after 73 days and hatching after 69 days of incubation. Some recorded incubation periods are: 59-60 days (Knepton, 1951:85), 64-67 days (Anderson, 1965:247), 77-78 days (Blanchard, 1921:54), and 78-81 days (Conant, 1934:66).

Lampropeltis triangulum.—The milk snakes constitute a highly variable polytypic species occurring over most of the United States and southward into northwestern South America. Gloyd (1928:119), Loomis (1948:121), Marr (1944:485), Werler (1951:44), Condit (1955:257), and Wright and Wright (1957:371) have published on its reproduction. Clutches of 5, 5, 6, 6, 6, 8, 8, 9, 11, 11, 11, 11, 12, 12, 12, 13, 13, 15, 15, and 16 eggs (average 10.2) are on record. Werler recorded a clutch laid June 5 that hatched July 24 and 25, and another laid July 21 that hatched August 26 and 28. Egg-laying has also been recorded on June 21 and July 3.

Lampropeltis zonata.—Stebbins (1954:402) mentioned a clutch of eggs of this Californian species that required 63 days for incubation in the laboratory. Cunningham (1959:18) mentioned a female that had three eggs on July 18.

Lamprophis

FitzSimons (1962:116, 118) stated that in southern Africa *L. inornata* lays six to 12 eggs in "early summer or around midsummer," and that *L. aurora* lays eight to 12 eggs.

Leimadophis

These small, oviparous Neotropical colubrines have long breeding seasons, and perhaps breed throughout the year. Sexton and Heatwole (1965:41) found gravid females of *L. epinephelus* containing 5 and 7 eggs on June 22 and 23 in Panama. Gravid females of *L. reginae* are represented in the Bassler Collection from Iquitos, Peru, for each month of the year, except for May, July, and October when no adult females were collected, and January and April, each represented by only one adult female. The 23 gravid females averaged 5.0 eggs; nine each had 5, three had 6, three had 7, two had 8, two had 3, two had 2, one had 4, and one had 1. In *L. taeniurus* from Iquitos, females averaged 3.88 eggs; five had 3, five had 5, three had 2, two had 4, and two had 6. These gravid females were from March, June, September, and October (Table 7), with small juveniles (118 to 128 mm snout-vent) from January (1), February (2), May (1), August (1) and December (1). A female of *L. bimaculatus* at Bogota laid 16 eggs on October 3 some of which hatched the next September 3, after the remarkably long incubation period of 11 months (Dunn, 1944:164).

At Rancho Grande, Estado Aragua, Venezuela, Test, Sexton and Heatwole (1966:42) found a female *Leimadophis zweifeli* with three eggs ready to be laid on April 8, and a female containing five large ova on July 4. A juvenile of

140 mm snout-vent, certainly not much larger than hatchling size, was found in December. Hence, it seems that breeding must occur through much of the year.

Leptophis

The members of this genus are racerlike frog-eating snakes of the Neotropical region. Information is available only for *L. ahaetulla.* Although the data are fragmentary, they suggest that in the equatorial lowlands there is some breeding throughout the year.

Leptophis ahaetulla.—Oliver (1947:5) studied a series of 83 of these snakes from Iquitos, Perú, in the collection of the American Museum of Natural History. He found that except for April when only one adult female was collected, and September and October when none was collected, there were gravid individuals from every month (Table 7). The samples were too small to attach much significance to the ratio of gravid to nongravid females. In the sample males and females were represented in almost equal numbers, and their numbers fluctuated in somewhat parallel fashion from month to month. It is remarkable that the catch for March was more than twice that for any other month, although according to Dr. Bassler's statement, cited by Oliver, human activity varied little. The trends for other kinds of snakes obtained in quantities were similar, and also showed the largest catches in March. Oliver pointed out that March was a month of high rainfall and of high water in the Amazon River, tending to concentrate the snakes on high ground, but the same statement applies to the months immediately preceding and following; other unknown factors must have been important in causing the large catch of snakes during March.

Lycodon

The Oriental house snakes are oviparous and seemingly have an extended breeding season where they occur in the tropics.

Lycodon aulicus.—This snake was studied by Wall (1909:87-101; 1921: 151-162), Lindberg (1932:695), Pope (1935:188), and Smith (1943:265). The latter stated that it lays from three to 11 eggs in a clutch, and possibly breeds twice per year. In the Deccan of northern India Lindberg saw gravid females in March, April, and May but farther south in the range egg-laying has been reported from February to October. A female from Hong Kong laid eggs on August 19 and they hatched on September 23. Wall reported gravid females in December (1), January (1), February (3), March (3), April (5), May (4), and June (3). He recorded clutches with 3, 3, 4, 4, 4, 5, 5, 5, 6, 7, 7, 8, 9, and 11 eggs, average 5.8. For six females that were from 24 to 29 inches in length, clutches averaged 7.84 eggs per clutch, whereas in eight that were from 18 to 23 inches long the average was 4.25.

Lycodon fasciatus.—Pope (1935:191), who cited earlier publications by Wall, stated that this snake produces four to 14 eggs. He mentioned a gravid female killed on June 6 and a hatchling found on September 19.

Lycodon laoensis.—Smith (1943:260) mentioned that a female from northern Thailand contained five eggs on April 3.

Lycodon rhustrati.—Pope (1935:195) mentioned a gravid female with four eggs, from Chungan Hsien, China, collected between July 9 and September 3.

Lycodon striatus.—In West Pakistan, Minton (1966:132) observed a mating pair on March 3; the female laid four eggs on April 18. Smith (1943:262) stated that two to four eggs are laid in July or August. Wall (1921:149) reported two gravid females and a clutch of eggs found in August.

Lycodon subcinctus.—This is a tropical species of southeastern Asia and the Malay Archipelago. Smith (1943:258) mentioned a record of a female from western Java that laid five eggs between May 20 and 24. These eggs hatched on August 11.

Lycodonomorphus

These snakes, found in aquatic or swampy habitats in Africa south of the equator, have cylindrical bodies with smooth scales. FitzSimons (1962:108) stated that *L. rufulus* in South Africa lays six to 10 eggs in "midsummer" and that they hatch about two months later.

Lycophidion

The African wolf snakes are small, smooth-scaled, short-tailed burrowers; seemingly they breed through much of the year in the tropics but have a more restricted breeding season in the Temperate Zone. In East Africa, Loveridge (1936:241; 1942:267) reported egg-bearing females of *L. capense* on December 9, February 21 to 28 (eight females), March 2, April 26 to 30 (four females), and June 30, and a clutch of eggs was found on February 2. In southern Rhodesia, Broadley (1959:16) reported a gravid female on December 16 and two on December 29. Nineteen clutches averaged 4.37 eggs with the following counts: 1, 2, 3, 3, 3, 4, 4, 4, 4, 4, 4, 5, 5, 5, 5, 6, 6, 7, and 8. FitzSimons (1962:127) stated that in southern Africa six to eight eggs are laid in "early summer." Possibly in the Temperate Zone, with seasonal restriction of breeding, the average size of clutch is greater than in the tropics, but more records are needed. These snakes are largely nocturnal and are usually found in rainy weather or in damp places. They are saurophagous, and seemingly subsist chiefly upon skinks.

Lytorhynchus

These are small, oviparous snakes that are widely distributed in desert regions of southwestern Asia and northern Africa, especially in sandy habitats. They are notable in having the snout modified for burrowing, as in many other desert snakes, especially those of the genus *Phyllorhynchus* in North America. There are several species, but they are rarely collected or observed, and little has been written regarding any of them. It is known that at least part of the diet consists of lizards.

Lytorhynchus paradoxus.—Minton (1966:130) reported that a female captured in West Pakistan laid two eggs on May 8, indicating that this is one of the least productive kinds of snakes.

Masticophis

The whip snakes are large, active, slender, oviparous colubrines of the southern United States, Mexico, and xeric regions in Central America and northern South America. They seem to conform to the breeding schedule typical of snakes living in the Temperate Zone. Whether there is ever more than one clutch per female per season is unknown.

Masticophis flagellum.—The coachwhip snake is a transcontinental species of the southern United States. Eleven clutches had 4, 7, 8, 8, 9, 10, 11, 12, 13, 13, and 16 eggs, average 10.1 (Force, 1930:26; Werler, 1951:41; Guidry, 1953:50; Wright and Wright, 1957:448; Carpenter, 1958:114; Cunningham, 1959:18). Some dates of laying are: June 6 and 19; June 20 to July 7; July 2, 7, 17, and 17. Guidry recorded that a clutch laid on July 17 hatched on August 30. Zweifel and Norris (1955:242) recorded a pair found mating on August 5, 1950 in Sonora. The female contained large eggs.

Masticophis lateralis.—For the California racer clutches of 6, 6, 6, 6, 6, 8, 8, and 9 eggs (average 6.9) have been recorded (Wright and Wright, 1957: 432; Perkins, 1943:111; Werler, 1951:41; Stebbins, 1954:379; Carpenter, 1958: 114; Cunningham, 1959:18). A female that mated on April 1 oviposited on May 27. Other dates of egg-laying are June 1, 24, 25 to 27, 28, and July 6. One clutch of eggs incubated in the San Diego Zoo took 94 days from laying till hatching.

Masticophis mentovarius.—Werler (1951:41) wrote that a whip snake of this large Mexican species laid 17 eggs from March 23 to 25. Alvarez del Toro (1960:157) stated that about 20 eggs are laid in early spring in Chiapas.

Masticophis taeniatus.—For the striped whip snake Gloyd and Conant (1934:13) recorded clutches of 3, 10, and 12 eggs in Texas; Wright and Wright (1957:455) recorded clutches of 9 and 8; Maslin (1947:138) recorded two clutches each with 4; Minton (1959:47) in southwestern Texas obtained a gravid female which laid eggs on June 1; hatching occurred on August 2.

Mehelya

The East African file snakes are ophiophagous and oviparous. The records suggest a spring breeding season, at least in the southern part of the range where there is cool winter weather. Loveridge (1939:143) mentioned a female of the Cape file snake, *M. capensis* found November 19, 1926, in a heap of plant debris and containing six eggs ready to be laid. In southern Rhodesia, Broadley (1959:18) mentioned a female that contained five large eggs on October 15. FitzSimons (1962:132) stated that there are five to eight eggs in a clutch.

Meizodon

Members of this African genus, the bush snakes, are near relatives of the European smooth snakes *(Coronella).* Little is known concerning the breeding habits. Neill (1964b:38) mentioned the genus as viviparous. Loveridge (1936:251) recorded a female *M. semiornata* from Kibwezi, East Africa, which had two oviducal eggs on March 29, 1934.

Ninia

These are small secretive Neotropical snakes. The limited information available for two of the species indicates an extended breeding season for both.

Ninia maculata.—I examined 64 coffee snakes in the University of Kansas Museum of Natural History from Costa Rica, mostly from Volcán Turrialba, but some had no date at all and others had such imprecise collecting dates as "summer of 1954." The smallest individual is 81 mm in snout-vent length, the largest 233 mm.

Six gravid females are 233, 231, 222, 218, 206 and 187 mm in snout-vent length. Specific dates recorded for their collection were June 2, 1951, and August 30, 1951 (for three). One that was dissected contained five eggs. Young of the following snout-vent lengths were collected in different months of the summer: June—111, 113, 137; July—104, 136; August—81, 89, 100, 103, 111, 113, 118, 135, 139, 152, 157, 158, 160, and 168 mm. Although only three months of the year are definitely represented in the collection, the distribution of gravid females and of young of various sizes indicates breeding throughout much of the year, if not all of it.

Ninia sebae.—Stuart (1948:77) found that in Alta Verapaz, Guatemala, this snake reached maturity at a total length of 250 mm, and gravid females were found from March to June. In early June a juvenile having an umbilical scar indicative of recent hatching, was captured. Later, Stuart (1958:24) recorded juveniles from Guatemala in mid-March and early April. In the Yucatán Peninsula, Gaige (1936:298) found that females contained eggs on July 13 and 14. Near Pichucalco, Chiapas, México, Burger and Werler (1954:647) found clutches of 2, 3, 3, 4, 4 eggs, all under the same log, on August 20. Alvarez del Toro (1960:170) wrote that in Chiapas the clutch consists of three or four eggs.

Opheodrys

Two species of green snakes occur in North America and several occur in eastern Asia. All are oviparous, with egg-laying in summer and hatching in late summer or autumn. Mating sometimes occurs in autumn (Richmond, 1956:325).

Opheodrys aestivus.—This is a species of the southeastern United States. Numbers of eggs reported in clutches are: 3, 4, 4, 4, 4, 5, 6, 6, 6, 7, 7, 8, 9, 9, 10, 11 and 12, average 6.76 (Wright and Wright, 1957:114; Carpenter, 1958: 114; Sabath and Worthington, 1959:32; Anderson, 1965:216). Tinkle (1961: 33) in southeastern Louisiana found an average of 4.7 (1 to 9) ovarian follicles more than 4 mm in diameter in snakes collected in winter. He suggested that these larger follicles represented the egg complements of the next breeding season. Tinkle obtained evidence that some females mature at the end of the first year and others at the end of the second year. Egg-laying has been reported for the following dates: July 8, 13, 20, 22, and August 1, 28 and 31. Additionally, Anderson recorded one clutch laid on July 4 that hatched September 6 and another laid June 24 that hatched September 22 and 23. Sabath and Worthington mentioned hatching of a clutch on July 21 and 22. In southeastern

Texas, Guidry (1953:52) recorded clutches laid June 17 and August 28 that hatched July 22 and October 20, respectively. Conant and Downs (1940:35) mentioned a Maryland female that on July 13 laid eggs which hatched on October 9 and 11.

Opheodrys major.—Pope (1935:285) reported females of this Chinese species containing 4, 6, 6, 7, 7, 7, 8, 8 and 13 eggs. Two collected on June 24 and 25 had eggs ready to be laid. Two others were taken between June 12 and July 20. Maslin (1950:454) reported a female taken on June 6 which contained 10 immature eggs. For the ten clutches reported by Pope and Maslin, average was 7.6.

Opheodrys vernalis.—In a study of 53 egg clutches of the smooth green snake in northern Michigan, Blanchard (1933:493) found an average of 6.7 ± .24. The eggs were usually laid in the first three weeks of August (average date August 10) and hatching occurred from August 5 to September 4, with approximately one-third of a month between laying and hatching. In the Chicago area Stille (1954:3) found an average of 5.8 ± .39 eggs in 25 clutches. Egg-laying occurred from June 24 to July 31 with an average date of July 16 or 17. An average hatching date of August 10 was obtained for the Chicago region. Wright and Wright (1957:558) mentioned 28 additional clutches from miscellaneous localities over the range, and the average was 7.18. There are records of copulation on August 18 and August 21 in Ontario.

Philothamnus

The bush snakes occur in the tropical and southern parts of Africa and are slender, elongate, smooth-scaled, and partly arboreal in habits. Records indicate that egg-laying occurs in early summer in the southern part of the range, and that there is a relatively long breeding season in the northern, tropical portion.

Philothamnus hoplogaster.—In East Africa Loveridge (1953:261, and 1958: 74) reported females containing oviducal eggs on October 1, October 9 to 29, November 11, December 12 (four females), December 18, December 23, January 5, February 20, February 25 and March 3 (two females). He noted that several others collected in December had no enlarged ova. In southern Rhodesia Broadley (1959:22) reported egg-bearing females on November 18 and January 20. Loveridge recorded a hatchling on February 12. Sixteen clutches averaged 5.50 eggs with counts of 3, 4, 4, 4, 4, 5, 5, 5, 6, 6, 6, 7, 7, 7, 7, and 8. FitzSimons (1962:149) stated that in southern Africa eggs are laid in early summer.

Philothamnus irregularis.—Loveridge (1942:272; 1953:262) reported gravid females from Bundibugyio, Mihunga, Misuku, and Kinsengi in central Africa on September 30, October 9, December 21, January 16, and February 10. They contained 5, 5, 7, 8, and 11 eggs. He noted that a native brought in 193 eggs from communal layings found in two termite nests on February 1. He stated (1958:80) ". . . in Uganda and western Kenya, from 4 to 8 eggs are laid toward the end of the lesser (November-December) or greater (February-March) rains, but that in the coastal belt of Kenya eggs are ready for laying about June." In Sierra Leone, Menzies (1966:172) obtained a female that

contained six eggs in September. In the same month he obtained another clutch of six eggs that were dug out of the ground; these hatched on October 5. FitzSimons (1962:146) stated that in southern Africa six to eight eggs are laid in December, January, or February, and incubation requires about two months.

Philothamnus natalensis.—FitzSimons (1962:151) stated that usually about six eggs are laid and that the young hatch in February.

Philothamnus semivariegatus.—Gravid females of the spotted wood snake reported by Loveridge (1936:248; 1958:126) from Kenya on May 8, June (no definite date) and June 30, and by Broadley (1959:26) in southern Rhodesia on January 26 contained unlaid clutches of 3, 3, 5 and 8 eggs. FitzSimons (1962:144) stated that there are six to 12 eggs per clutch.

Phyllorhynchus

These small, nocturnal, oviparous, leaf-nosed snakes inhabit the southwestern United States and México. Little is known about their reproduction, but the records suggest that normally a female produces only one clutch per year, in early summer. Brattstrom (1953:62) reported on *P. decurtatus* obtained over a 20-year period in San Diego County, California. Females containing large eggs were obtained chiefly in June (11 records) and July (3 records) but with one record each for April, May and August. On the basis of size groupings, the smallest fecund female (325 mm) was thought to be in her third season of growth. Stebbins (1954:369) stated that from two to four eggs are laid.

Pituophis

These are large, oviparous snakes that occur over a wide range of climatic conditions from Canada to Guatemala. Spring breeding, early summer egg-laying and autumn hatching is the rule. In captivity, under favorable conditions, females are capable of producing two clutches of eggs within a season.

Pituophis melanoleucus.—This polytypic species, as now conceived, has divergent subspecies including *melanoleucus* of the eastern United States, *sayi* of the Great Plains, and *catenifer-deserticola-annectens-affinis* of the western states and adjacent Canada and México. Obviously seasonal schedule is somewhat affected by latitude in such a wide-ranging species. Wright and Wright (1957:592, 595, 598, 602, 611, 618) listed 49 clutches of eggs which averaged 9.7 per clutch (3 to 22). These showed some evidence of geographic variation; eight from the southeastern states (subspecies *melanoleucus* and *mugitus*) averaged 8.0 (4 to 12), 13 of *sayi* averaged 12.4 (5 to 19), and 29 clutches of the western subspecies averaged 8.9 (4 to 24).

Fisher (1925:108) mentioned an instance of copulation in captive *catenifer* on April 21 and 29 and eggs were laid on August 7 and 8. Cowles (1935:44) wrote that a pair of *deserticola* courted in late May and eggs were laid on August 8 and 9. Klauber (1947:58) mentioned dates of laying ranging from July 7 to August 17 in ten clutches in southern California *(affinis, annectens),* and for these same clutches incubation periods averaged 66½ (64 to 71) days.

Conant and Downs (1940:39) reported a clutch of *melanoleucus* eggs laid July 12 which hatched September 19, and another clutch laid July 13 hatched

September 18 to 20. New (1953:182) reported a clutch of the same subspecies laid June 28 which hatched September 11 and 13.

Of outstanding interest are breeding records of this species kept by Charles E. Shaw at the San Diego Zoo which he kindly made available to me. One snake, an albino female *(P. m. annectens)* received at the zoo as a juvenile in May 1940, produced clutches of eggs (always 3, 4, or 5) on the following dates: July 3, 1943, May 27, 1944, July 3, 1945, May 13, 1946, May 20, 1947, May 29, 1948, July 4, 1949, May 4, 1951, May 12, 1952, April 29, 1954, April 16, 1955, June 23, 1956, and April 28, 1957. She died in December 1957. It is notable that she produced a clutch annually—with a range of several weeks in the date—except in the years 1950 and 1953, when she failed to produce. Her unusually small clutches may have been in some way correlated with the genetic abnormality involved in albinism.

A captive-bred albino, daughter of the above snake, had the following breeding history, summarized from Shaw's notes:

September 1945	Hatched at zoo
May 1947, April, July and August 1948, and March and April 1949	Courted
May 17, 1949	Mated
July 2, 1949	Laid three eggs
February and March 1950	Courted
April 6 and 8, 1951	Mated
May 10 to July 10, 1951	Laid 5 eggs, each on a different day
April 13, 17, 19, and 28, 1952	Mated
April 28 and May 29, 1952	Laid one and 4 eggs on these two dates
April 25, 1953	Mated
June 13, 15, 16 and 19, 1953	Laid 1, 1, 2 and 2 eggs
April 7, 9 and 17, 1954	Mated
May 31, 1954	Laid 3 eggs
May 7 and 15, 1955	Laid 1 and 3 eggs
May 23 and 24 and June 1 and 3, 1959	Laid 1 egg on each date
June 11, 1959	Died

A pine snake hatched at the zoo on July 15, 1940, was successfully reared and produced clutches of 4 or 5 eggs on the following dates: February 10, 1943, April 24, 1945, March 18, 1946, April 29, 1946, February 1, 1947, May 16-17, 1948, April 2, 1949, April 12, 1950, and April 11, 1951. Another captive-bred pine snake hatched on May 31, 1946, was kept in isolation until January 1954 then placed with other pine snakes including a male. In 1955 it laid two clutches, of 6 and 7 eggs, on March 17 and November 4, respectively.

Another series of records was obtained from three female pine snakes from the same clutch of eggs, which hatched at the zoo on April 25, 1941. On April 27, 1945 eggs appeared in the cage, laid presumably by just one of the three, but it was not known which. Number 1 produced clutches on: April 12 and 13, 1946, March 12, 1947, May 4, 1947, March 13, 1948, March 14 and 15, 1949, March 29, 1950, and April 11, 1952. Number 2 produced eggs on April 4, 1948 and April 12, 1949. Number 3 produced eggs on April 20, 1946, April 1-4, 1947, May 23, 1947, April 5, 1948, April 12, 1949, May 1, 1950 and April 22, 1952. It is notable that two of these females both produced second clutches in 1947, and that from time to time any of the females might pass an entire year with no egg production. There was notable difference in the pro-

ductivity of these siblings, presumably resulting from the varying amounts of food taken by them.

These records of captives must be used with caution in attempting to reconstruct breeding cycles under natural conditions. Nevertheless, they are of extraordinary interest in several respects. They show a strong tendency to maintain an annual breeding cycle. They indicate breeding maturity is only attained in the third or fourth year in *Pituophis*. They demonstrate a potentiality, even in these relatively northern snakes, to produce a second clutch of eggs within a few weeks of the first one, under favorable conditions. They indicate that the female snakes, even established breeders, living under favorable conditions and free of debilitating disease or injury, tend to skip a year occasionally in their annual egg-production.

Plagiopholis

These are small, terrestrial and rather secretive, earthworm-eating colubrines of the Oriental region. Maslin (1950:439) mentioned females of *Plagiopholis styani* collected in Kiangsi, China, in May and on June 7, which contained 6 and 8 enlarged eggs. Pope (1935:180) mentioned additional complements of 5, 6, 7, and 11 eggs.

Prosymna

Loveridge (1936:255; 1958:160) reported gravid females of the East African shovel-snout *(Prosymna ambigua)* with oviducal eggs on May 28, November 23, December 23, January 5, January 16, and February 23, and a hatchling on October 4. Clutches had 3, 3, and 14 eggs. These meager records indicate a long breeding season. In East Africa at Livale, Loveridge (1958: 168) reported a female of *P. pitmani* containing four large eggs on June 6. FitzSimons (1962:155) stated that clutches of *P. lincata* average three or four eggs.

Pseudaspis

The mole snake *(P. cana)* is a medium-sized, burrowing, viviparous colubrine of South Africa. Brain (1959b:71) described a mating observed in February, 1958. Rose (1929:156) stated, "The progeny are born alive, very small and exceptionally numerous, as many as 80 being produced at a time." FitzSimons (1919:100-101) stated that there are usually 30 to 45 young and he included a photograph of a female with her brood of 84 young. FitzSimons (1962:165) stated that male mole snakes fight during the October mating season, and that the young, averaging 30 to 50 per litter, are born in March or April. He mentioned a record litter of 95 young born at the London Zoo.

Ptyas

The Asiatic rat snakes are large oviparous colubrines that are primarily tropical. The observations cited below indicate that, near the equator at least, their breeding extends throughout much of the year and that individual females are capable of producing at least two clutches per year.

Ptyas korros.—The Indian rat snake, a large racerlike species, is widely distributed in southeastern Asia and the Malay Archipelago. Pope (1935:219) summarized several notes concerning its breeding. He mentioned four egg clusters with about nine eggs apiece found in Kwangtung China in late May and early June. Hatchlings were found there in early September. A female killed near Rangoon, Burma, on June 3 contained nine eggs. Gravid females from Assam, northern India, May 13 to June 4, contained 1, 3, 4, 5 and 6 eggs. A clutch of nine eggs found in Java on August 22 hatched on October 29. In Malaya, Kopstein (1938:164) found one gravid female in February, one in June and three in December. One female that he kept in captivity produced two clutches with a 70-day interval intervening.

Ptyas mucosus.—Like the preceding, the dhaman is a large rat snake of southeastern Asia and adjoining areas. Pope (1935:222) citing earlier publications by Wall, stated that the clutch consists of nine to 14 eggs, and that after oviposition the female coils around them to guard them. In India, McCann (1937a:424) observed mating in April, May and June, and noted females with oviducal eggs in June and July. Smith (1943:162) stated that in India mating takes place in the hot weather—May or June—and eggs are deposited in August or September. Wall (1921:181) noted pairing in June and July, and gravid females as follows: May (4), June (3), July (12), August (2), and November (1). He reported hatching in September (3 instances), October (once) and December (once). In an earlier publication the same author (Wall, 1906:268) listed clutches as follows: 9, 9, 10, 11, 12, 12, 12, 13, 13, 13, 14, 14, average 11.8. Kopstein (1938:164) in Malaya reported gravid females in February (1), June (1), September (1), October (2), November (2) and December (2). He reported that a female kept in captivity produced two clutches with a 59-day interval intervening. He found that both sexes attained sexual maturity approximately 20 months from the time of hatching. Both this and the preceding species were among the "rice field snakes" which, Kopstein found, did most of their egg-laying in the rainy season—November through April.

Rhadinea

These small, oviparous snakes have many Neotropical species, and one species, the yellow-lipped snake *(R. flavilata)* inhabits Florida. Myers (1967: 67) reported clutches of 2, 3, 3, 3, 3, 4, 4, and 4 eggs, average 3.25. Dates of oviposition were June 4, July 6, July 19 and August 19, indicating a long breeding season with a possibility of more than one clutch per female.

Rhinocheilus

The long-nosed snakes are confined to desert regions of the southwestern United States and northern Mexico, where they conform to the usual breeding schedule of snakes in the Temperate Zone. Klauber (1941:323), Stebbins (1954:407), Woodin (1953:290), Shannon and Humphrey (1963:155) and Lardie (1965:366) have published notes concerning the reproduction of *R. lecontei.* These authors have reported clutches of 4, 5, 5, 6, 6, 6, 7, 7, 7, 8 and 9 eggs, average 6.36. Shannon and Humphrey mentioned a clutch laid on July 11 that hatched on September 30. Lardie mentioned a clutch laid on

June 11 that hatched on August 15. A female kept by Woodin laid eggs in the first week of July, another laid August 15-16. The spread of more than two months in laying dates in this small sample suggests the possibility that more than one clutch per season is produced by some females.

Salvadora

The patch-nosed snakes are racerlike colubrines confined to the southwestern United States and northern México. They are oviparous. The few recorded dates of egg-laying show such a wide span that production of two or more clutches per season by an individual female seems possible, but it remains to be demonstrated.

Salvadora grahamiae.—Conant (1942:196) reported that a female from near Palo Pinto, Texas, laid 10 eggs on April 1, 1941. Several of these hatched August 4 to 10. Conant and Downs (1940:36) mentioned a clutch of six eggs. Minton (1959:47) stated that a female collected April 1 deposited six eggs on May 29, and these hatched on August 27 and 28.

Salvadora hexalepis.—Wright and Wright (1957:654, 659, 661) summarized notes of several earlier authors. One pair mated in captivity on April 14, another pair in June. Gravid females with large eggs have been reported in May (no specific date), May 31, June 4, and August 22. One female contained five eggs and another had 10.

Scaphiophis

The beaked snakes are an African genus modified for fossorial life and having the snout chisel-like in form. In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman, and Chapman (1962:429) found that females of S. *albopunctatus* collected in January, March and April (one in each month) had only small ova, but that in May two had ova 9 mm long and that in July four contained large eggs 20 to 41 mm long.

Sonora

The ground snakes are small, somewhat secretive, oviparous, and inhabit arid regions in the southwestern United States and México. One species, S. *episcopa,* has been studied rather intensively under natural conditions. Over a 22-year period Kassing (1961:185) examined 1201 of these Great Plains ground snakes from the vicinity of Tulsa, Oklahoma, and Palo Pinto, Texas. She found that mating occurred in May and June and sometimes, seemingly, in fall. There were 148 eggs in 36 gravid females, an average of 4.1 per clutch. Some of the eggs that were incubated in the laboratory hatched in 53 to 67 days, but 84.6 per cent of the eggs spoiled within 24 days. The snakes were found to reach maturity at an age of 1½ years. In the Texan population egg-laying was concentrated in the period from June 3 to 5, and in the Oklahoman population it occurred chiefly from June 19 to June 21. In Missouri breeding is somewhat later than in Texas and Oklahoma; Anderson (1965:257) mentioned the following clutches laid in captivity: five eggs on June 22, four eggs on June 25, six eggs on June 29, four eggs on June 26. Anderson observed courtship in

recently captured snakes on June 24, and he found a copulating pair under a rock on September 21, thus obtaining evidence that there is both spring and autumn breeding.

Staedeli (1964:581) obtained a female vermillion-lined ground snake, *S. semiannulata*, from the Imperial Valley near El Centro, California, on August 22, 1963. Three days later it laid a clutch of four eggs, and these hatched on October 20 after a 56-day incubation.

Spalerosophis

These slender, racerlike, desert-living colubrines of southwestern Asia and North Africa inhabit a region of sharply defined seasonal change, with winter dormancy. The production of two clutches of eggs per season, and production of a second clutch as late as mid-September is rather surprising, but observations on *S. diadema* have revealed these capacities.

Spalerosophis arenarius.—Minton (1966:127) reported that a large female killed in West Pakistan on October 3 contained 10 eggs, apparently almost ready to be laid.

Spalerosophis atriceps.—Minton (1966:125) reported the breeding history of a pair from West Pakistan kept in captivity. They mated on the nights of March 11 and 12 and the female laid three eggs on May 29 and a fourth a week later. The next year they mated on April 20 and 21 and the female laid three eggs on May 9. The third-year mating was not observed but the female laid five eggs on May 9. Another captive female laid eight eggs, October 25-26.

Spalerosophis diadema.—The diadem snake of Arabia and North Africa was studied by Dmi'el (1967:332) in Israel. In 21 clutches he found an average of 8.0 (3 to 16) eggs per clutch. His records seemed to indicate an interval of approximately 50 days between copulation and oviposition in captivity. He found in a study of captive individuals that efficiency in utilization of food decreases with age, and that the older females are not able to maintain their weight after successive clutches have been produced. It is remarkable that, occasionally at least, a second clutch may be produced within the same season; a ". . . female collected in the middle of May, 1960, laid a first clutch of 8 eggs on June 8, 1960. This particular female was subsequently kept in isolation and laid a second clutch of 8 eggs on September 3, 1960."

Toluca

These small Mexican colubrines are closely related to snakes of the genus *Conopsis*, and like them are limited to high altitudes, and are viviparous. Greer (1966:372) examined several gravid females of *T. lineata* and established the fact that this species is viviparous. There were 2, 3, 3, 3, 3 and 5 embryos, some nearly ready for birth and enclosed only in a thin, transparent membrane. Two of the females were collected in Veracruz in January. Others were from Hidalgo, and no dates were recorded for them.

Tretanorhinus

These are Neotropical water-loving snakes often found in mangrove swamps. A gravid female of *T. variabilis* from Candelaria, Cuba, and kept by Petzold

(1967:243) at the Berlin Tierpark, laid eight adherent eggs on August 1, and four of these hatched after an incubation of 35 days.

Opisthoglyphous series

The following colubrid genera are more or less venomous, rear-fanged snakes that often have been grouped as a subfamily Boiginae, but the group is now considered to be an unnatural one and some of the genera are believed to be more closely related to genera of aglyphous colubrines than they are to each other. Nevertheless some of the genera constitute natural groups that are closely related. Underwood (1967:110) retained the subfamily Boiginae for the genera *Boiga, Imantodes, Leptodeira, Psammodynastes, Tachymenis,* and *Telescopus,* but he placed it in the family Homalopsidae, along with homalopsine and dasypeltine rear-fanged snakes. Most of the opisthoglyphous colubrines formerly considered boigines are tropical or subtropical in distribution, and they are well represented in South and Central America, Africa, and Asia, but they enter the Temperate Zone in both hemispheres. Nocturnality and/or arboreal adaptation are especially common. In the Old World genera, oviparity is the usual condition and only *Ahaetulla* and *Psammodynastes* are viviparous. Bailey (1966:886) stated that he had seen advanced embryos or recently born broods in the South American *Tomodon dorsatus, Tachymenis peruvianus, Ptychophis flavovirgatus,* and at least seven species of *Thamnodynastes,* and that none of these genera is known to have oviparous species. He stated that these genera form a closely knit suprageneric group, which probably also should include the genera *Calamodontophis, Gomesophis,* and *Pseudotomodon* and that probably all these are viviparous. However, a larger number of Neotropical genera are exclusively oviparous. In some of these tropical opisthoglyphs the breeding season is known to be long, extending through much of the year.

Ahaetulla

These slender, arboreal, saurophagous, tropical Asiatic whip snakes are slow-moving, and are remarkable in being viviparous. Seemingly breeding may occur through much of the year or all of it.

Ahaetulla nasuta.—For the common green whip snake of India, Wall (1921:298) recorded gravid females or birth of young on the following dates: March 31, April, May (2 gravid; 2 gave birth), August, September (2 gravid), December 3 (one gave birth to young). Smith (1943:378) stated that from three to 22 young are born at a time and this may occur in any month from March to December. Wall (1905:548) mentioned litters or complements of

embryos or eggs numbering 3, 4, 5, 5, 12, and 8. The last record involved a female in the London Zoo which was received ". . . from Java on the 15th of August, 1885, gave birth to 8 young on January 9th, 1888, having had no male companionship during this whole period."

Ahaetulla perroteti.—Wall (1919) reported nine gravid females collected in the Nilgiri Hills of southern India between July and the beginning of September.

Ahaetulla prasina.—Smith (1943:376) obtained a female from southeastern Thailand, which contained young almost ready to be born on July 1. Pope (1935:323-324) mentioned gravid females from Burma and Upper Assam containing 3, 7 and 9 eggs. One was secured May 23, another on June 5 and the third in late March or early April.

Aparallactus

The centipede-eaters are small, secretive snakes with slender cylindrical bodies, occurring in southern and eastern Africa. FitzSimons (1962:270) stated that in *A. capensis* there are two to four eggs per clutch. Loveridge (1936:270) recorded a female of the East African *A. ulugurensis* having two oviducal eggs on June 17, 1934. Loveridge (1942:300) also recorded a female of *A. modestus* containing two large eggs on November 13, 1938.

Boiga

This genus of rear-fanged snakes includes a rather diverse group of species, the tree snakes, mangrove snakes and gammas, in tropical Africa, Ceylon, India, Malaya, and the East Indies.

Boiga ceylonensis.—Wall (1921:279) found gravid females of this species in May (1), August (3), and September (5).

Boiga forsteni.—Wall (1921:289) noted gravid females of this Indian snake in August and September. Smith (1943:359) cited the authority of local snakemen for the statement that the female lays seven to nine eggs in the hot weather.

Boiga multomaculata.—Pope (1935:331) cited observations on the blotched snake in Hainan and Burma. He mentioned females containing 5, 6, 7, and 7 eggs. At Rangoon one was reported depositing eggs on April 19. A female from Burma contained eggs nearly ready to be laid on August 21. Obviously the breeding season is lengthy.

In Malaya, Kopstein (1938:163) reported that a captive female laid a clutch of four eggs on October 22, 1936, and produced a second clutch of four just 60 days later on December 21. A second female produced two fertile clutches of four eggs each on May 5, 1934, and January 1, 1935. Kept in isolation it subsequently produced only infertile eggs.

Boiga pulverulenta.—Schmidt (1923:62) recorded that one of these snakes in the Belgian Congo contained large eggs (29 × 11 mm) in June 1914.

Boiga trigonata.—Wall (1908:546) reported females of the Indian gamma containing 3, 5, 6, and 10 eggs. The same author (1921:273) reported gravid females in May (1), June (1), July (2), August (1), and September (1) in

Ceylon. In the Deccan of northern India, Lindberg (1932:695) noted gravid females in May, June, and July. Smith (1943:350) stated that from three to 11 eggs were laid. Minton (1966:139) reported that in West Pakistan, hatchlings were observed from late September to early November and that a female laid eight eggs on August 28, some of which hatched on October 30. Another female contained 11 eggs on August 31.

Chrysopelea

The flying snakes of the Malayan Region and adjacent southern China are active, arboreal and oviparous. Smith (1943:254) stated that at Bangkok, Thailand, *C. ornata* mates in June, and lays from six to 12 eggs. Pope (1935: 320) stated that near Rangoon, Burma, egg-laying was in June. Wall (1908: 236) reported females with complements of 6, 9, and 11 unlaid eggs.

Coniophanes

These small, nocturnal, terrestrial, oviparous snakes are mainly Neotropical, but extend north as far as southern Texas. Livezey and Peckham (1953:175) wrote that a female *C. fissidens* collected in San Marcos, Guatemala, in May 1951 contained two eggs. Brown (1937:234) wrote that a female of the black-banded snake, *C. imperialis*, collected in March near Harlingen, Texas, laid three eggs. Werler (1949:60) kept one from near Brownsville, Texas, which on May 3 and 4 deposited five eggs. Alvarez del Toro (1960:154) wrote that in Chiapas, México, this snake lays about 10 eggs which require 40 days incubation. Stuart (1958:24) reported a female from El Petén, Guatemala, containing well-developed eggs in mid-May, and reported juveniles in mid-February and early March.

Conophis

These are active, terrestrial, saurophagous snakes of arid areas in México and Central America. They are oviparous. Alvarez del Toro (1960:154) wrote that in Chiapas the female of *C. vittatus* lays five to ten eggs in early spring.

Crotaphopeltis

These nocturnal, oviparous, frog-eating snakes are widely distributed in Africa and breed at various times of year. In the Belgian Congo, Schmidt (1923:109) reported an African white-lipped snake, *C. hotamboeia* that contained large eggs in July. Loveridge (1936:259, 1942:289, 1953:259) reported several gravid females from East Africa: on March 31, June 4, June 15, June 16, June 17, June 17, June 26, and December 18. Eggs numbered 3, 4, 5, 5, 6, and 10, average 5.5. The records suggest year-round breeding. However, in southern Africa FitzSimons (1962:191) stated that the eggs, six to 12 per clutch, are laid in spring or early summer. Incubation requires about three months. Mating was observed in November.

Dispholidus

The boomslangs are dangerously venomous, active and arboreal rear-fanged snakes widely distributed in the tropical and southern parts of Africa. Loveridge

(1953:282) noted that a *D. typus* from Kasunga, Nyasaland, had 14 ova, August 19 to 23. Others collected in December, January, February, and March were not gravid. Robertson, Chapman and Chapman (1962:430) mentioned a female from the Rukwa Valley in Tanganyika in May which had 17 well-developed ova 25 × 15 mm. In South Africa, FitzSimons (1919:154) reported that a female laid 13 eggs in October. In southern Rhodesia, Broadley (1959: 36) reported a pair in copulation January 29, 1956. FitzSimons (1962:200) stated that in southern Africa the eggs, usually 10 to 14 per clutch, are laid from late spring to midsummer, and their incubation requires from four to seven months.

Hypsiglena

These small, secretive, terrestrial, nocturnal snakes of arid regions in the western United States and México seem to have an extended breeding season. Hibbard (1937:74) reported that a female night snake, *H. ochrorhyncha,* captured in southwestern Kansas on June 12, 1936, contained four eggs. Stebbins (1954:459) wrote that a female from western Oklahoma laid six eggs on July 7, and a female from Zapata County, Texas, captured on March 10, laid four eggs on April 25. Two of the latter eggs hatched on June 18.

Imantodes

These are remarkably slender and elongate arboreal snakes of tropical South America and Central America. Available data suggest a long breeding season, at least in equatorial rain forest. Stuart (1948:80) reported that blunt-headed tree snakes, *I. cenchoa* collected in late April and in mid-June in Alta Verapaz, Guatemala, contained well-formed eggs. I examined 42 specimens from Iquitos, Perú, in the American Museum of Natural History. The only gravid female was collected in January; nongravid adult females were from February (2), April (1), and July (2). Juveniles of less than 300 mm snout-vent were collected as follows: February, 264 mm; March, 253 mm; August, 210 mm; September, 269 mm. Although it is inadequately small, the sample suggests a long breeding season. The single gravid female that was examined contained two elongate eggs.

Alvarez del Toro (1960:160) wrote that in Chiapas, México, *I. splendidus* lays four to eight eggs.

Leptodeira

These are oviparous, Neotropical snakes with arboreal tendencies. There is some evidence of breeding throughout the year in the equatorial Peruvian rain forest, but for México and Central America records of gravid females are most concentrated in spring. A captive female, of unknown origin but probably from Central America, produced a clutch of eggs at about the same time—late March to early May—in several different years (Haines, 1940:116).

Leptodeira annulata.—I examined extensive series from Iquitos, Perú, in the American Museum of Natural History Bassler Collection . There were 111 that had recorded dates, at least to the month. Juveniles less than 200 mm in snout-

vent length, and probably not more than a few weeks old, were recorded as follows: February, 185 and 157 mm; March, 182 mm; June, 174 mm; August, 186 and 155 mm; October, 171 mm; December, 161 mm. Gravid females were taken in every month except April, May, and July, hence, seemingly there is breeding throughout the year. In 34 females eggs averaged 4.0; 16 had 4, nine had 5, five had 3, three had 2, and one had 7. Livezey and Peckham (1953: 175) mentioned a female of another subspecies (possibly another species), taken in Guatemala, that contained 10 eggs in May. Taylor (1949:12) reported one from San Luis Potosí, México, that contained nine eggs.

Leptodeira frenata.—Stuart (1935:53) reported a specimen from El Petén, Guatemala, that contained seven mature eggs on April 19.

Leptodeira maculata.—Duellman (1958:115) reported one from western México that was gravid on June 18. He reported an incubation period of 57 days for two eggs kept under artificial conditions. Alvarez del Toro (1960:165) stated that five to eight eggs are laid, in winter.

Leptodeira punctata.—Duellman (1958:115) mentioned a gravid female of this species collected in western México on August 17 or 18.

Leptodeira septentrionalis.—Haines (1940:116) published a remarkable series of observations on one of these snakes accidentally shipped with bananas from Central America to Detroit, Michigan, in March 1934. It was acquired by Haines in August, 1934. It produced clutches with fertile eggs on March 20, 1936, May 6, 1938, and March 29, 1939. There were seven, six, and nine eggs in these three clutches. It is notable that the snake tended to have an annual cycle of reproduction with egg-laying in spring, but that it missed 1935 and 1937, that it was seemingly sexually mature and already inseminated when acquired, and that the original supply of spermatozoa persisted and remained viable for at least five years. The snake increased in length from 750 to 960 mm during the period of its captivity. Duellman (1958:115) mentioned gravid females of this snake collected on February 11, March 20, March 22-28, May 6, and May 7-14. He reported an incubation period of 79 days for eggs deposited by a captive female. Neill (1962:239) mentioned a hatchling from British Honduras still retaining an umbilical scar on August 28 and probably hatched in the same month.

Leptodeira splendida.—Duellman (1958:115) mentioned a gravid female from western Mexico collected on February 20.

Macrelaps

These small-headed, smooth-scaled, cylindrical, African, burrowing and secretive snakes have reduced dentition, but with relatively large fangs and potent venom. FitzSimons (1962:263) stated that in the Natal black snake, *M. microlepidotus,* the clutch of three to eight eggs is laid about midsummer.

Oxybelis

The American vine snakes are oviparous, slender, active and scansorial; they occur from southern Arizona southward through tropical South America. In

Panamá, Sexton and Heatwole (1965:40) found a clutch of four eggs of *O. aeneus* in a depression in leaf litter on July 1. These eggs hatched on July 13. At the northern end of the range in Arizona, Stebbins (1954:454) reported a clutch of four eggs for the same species. Sexton and Heatwole obtained a gravid female of *O. brevirostris* containing three eggs, in Panamá on March 18, 1963. Stuart (1948:82) reported a female of *O. fulgidus* having well developed eggs in mid-April in Alta Verapaz, Guatemala.

Oxyrhopus

These are slender, terrestrial, Neotropical, ophiophagous snakes. The Bassler Collection from Iquitos, Perú, had gravid females of *O. petolus* collected in March, September, and November. These females contained 5, 6, 6, 6, 8, 10 and 10 eggs, average 7.3. The five smallest individuals, those judged to be only a few weeks old, were collected in November, December, January, and June. Test, Sexton and Heatwole (1966:43) wrote that a female from Rancho Grande, Estada Aragua, Venezuela, laid seven eggs June 1 and 2, and two of the eggs hatched September 1-2.

Psammodynastes

The small, active, mock viper, *P. pulverulentus* is widely distributed in southeastern Asia, and is described as both nocturnal and diurnal, terrestrial and arboreal, and of vicious disposition. Wall (1910:76) stated that in the hill country of northern India mating is probably in August but in the plains the breeding season is from December to February. He mentioned females containing 6, 8, 10, and 10 eggs. Pope (1935:326) summarized the known facts concerning its reproduction. He stated that the young per litter average six (3 to 10). He mentioned a female containing small embryos when taken at Yanping, China in May, a recently born individual at Rangoon, Burma in June, females with advanced embryos in August, and a gravid female at Kutkai, in northern Burma on October 8. In Thailand, Taylor and Elbel (1958:1146) obtained a gravid female containing seven eggs on February 22. Obviously the breeding season extends throughout much of the year, at least if the range as a whole is considered. Gravid females of *O. melanogenys* were taken at Iquitos in January (1), March (3), June (1), September (1), and November (1); see Table 7. Ten contained 5, 7, 7, 8, 8, 8, 9, 9, 9, and 11 ova.

Psammophis

The sand snakes are terrestrial and oviparous and occur in grassy or sandy habitat.

Psammophis angolensis.—Pienaar (1966:193) reported that in Kruger National Park, South Africa, the pygmy sand snake produces a clutch of three to five eggs.

Psammophis biseriatus.—Loveridge (1940:59) noted that young appearing to be recently hatched, 300 mm or a little more in length, were found in Tanganyika in December.

Psammophis schokari.—Minton (1966:141) noted that in West Pakistan hatchlings were found from early July through most of September. Females contained six and five eggs on April 6 and May 1.

Psammophis sibilans.—In southern Rhodesia, Broadley (1959:46) reported that a female sand snake laid 10 eggs on October 2, 1957, and these hatched on February 22, 1958. In East Africa, Loveridge (1940:38) reported gravid females on the following dates: November 29, December 13, December 21, January 18, and January 18. There were 4, 7, and 10 eggs in different females. In southwestern Tanganyika, Robertson, Chapman and Chapman (1962:428) noted that a female taken in July had 26 large (21 × 7 mm) eggs whereas two others taken in November and December had only minute ova. In Sierra Leone, West Africa, Menzies (1966:175) obtained a clutch of eggs that were dug out in March and contained large embryos. FitzSimons (1962:231) stated that in southern Africa the eggs, usually 10 to 15 per clutch, are laid in December or January.

Psammophis subtaeniatus.—Loveridge (1940:53) reported gravid females in East Africa on September 23, and October 22 (5 females). There were 6, 6, 7, 8, and 10 eggs. Sixteen recently hatched young were found on December 10 and January 1. In southwestern Tanganyika, Robertson, Chapman and Chapman (1962:429) obtained two females in September and one in October which had enlarged oviducts as if they had oviposited recently, but six in the period March to July and eight in November and December had only small ova. Complements of 9, 20, and 20 eggs were recorded.

Psammophylax

These are small, active, terrestrial African snakes. FitzSimons (1962:213) stated that in the South African *P. rhombeatus* the eggs, up to 30 per clutch, are laid in midsummer, with embryos already partly developed, and the female coils around them and guards them for the five or six weeks of incubation. Loveridge (1942:290, 1953:273) reported two gravid females of the striped skaapsteker, *P. tritaeniatus,* containing eight and nine large eggs, on the Lichenya Plateau in Nyasaland on August 10, and two other gravid females from an altitude of approximately 10,000 feet in late October. Broadley (1959:43) mentioned a captive female which laid four eggs November 27 to 30, and then died with 10 more eggs still unlaid. FitzSimons (1962:215) stated that in *P. t. tritaeniatus* in South Africa, the clutch is 6 to 10 eggs. The species covers a wide range geographically and altitudinally; doubtless there are geographic differences in size of clutch and timing of breeding season.

Both *P. rhombeatus* and *P. tritaeniatus* subsist on a variety of small vertebrates such as frogs, lizards, birds and rodents. However, *P. rhombeatus* is a larger and much more active species, which has a more potent venom. According to FitzSimons the venom is neurotoxic like that of South African elapids, but is reputed to be even more powerful, weight for weight. Seemingly the habit of guarding the eggs has been recorded only in the species *rhombeatus.*

Rhamphiophis

These beaked snakes are oviparous, terrestrial colubrines of central and eastern Africa. Loveridge (1936:263) recorded three gravid females of *R. oxyrhynchus* at Sipi and Bukori in East Africa on December 13 and January 18; there were 4, 10, and 17 eggs.

Tachymenis

These are small to medium-sized, rather stout-bodied, viviparous, rear-fanged, South American colubrids having fairly potent neurotoxic and haemolytic venom. Donoso-Barros (1966:403) stated that in *T. peruviana* in northern Chile, females are carrying enlarged eggs in May and young (usually six to eight per litter, sometimes as many as 10) are born about October.

Tantilla

These are small, burrowing or secretive snakes that are widely distributed in the southern half of the United States and occur southward into the Neotropical Region where there are many species. They are oviparous and are notable for the small size of the clutch, with usually one, two or three eggs. Seemingly it is normal for the female to ovulate a larger number but to resorb some of them from the oviducts. Within the United States these snakes seem to conform to a breeding schedule typical for the Temperate Zone, but in the tropics there is deviation from this schedule.

Tantilla coronata.—The crowned snake is a small, burrowing species of the southeastern United States. Neill (1951:59) wrote of finding mating pairs frequently, in April or May, beneath scant cover at the bases of rotting stumps, on the outskirts of Augusta, Georgia. He found one nest with three eggs. Cook (1954:31) in Mississippi also recorded a gravid female with three eggs. Minton (1949:147) stated that a female from Indiana contained two or three ova which were visible through the partly translucent body wall. Neill and Boyles (1957: 78) examined three gravid females collected in May in Tuscaloosa County, Alabama. Each female had in her oviducts three elongate eggs (11 to 23.7 mm) and in addition had five to nine small abortive eggs or yolks of more or less rounded shape, one to four mm in diameter.

Tantilla gracilis.—In northeastern Oklahoma, Force (1935:649, 651, 658) found that the population of the flat-headed snake in spring included besides the reproductive females, some that were obviously first-year young (95 to 125 mm, with ova of microscopic size), and others that were intermediate in size with somewhat larger immature ova, and were taken to be second-year young. The first half of May was found to be the mating season, and clutches of eggs were deposited by females in confinement on June 13, 18, 19, 22, 25 and 26. Usually there were either two or three eggs in a clutch, but complements of one and four were noted. Eggs incubated in the laboratory hatched on September 7, 14, and 17—83 and 84 days after oviposition. Carpenter (1958:115) and Anderson (1965:259) reported additional clutches with 2, 2, 3, and 3 eggs. Two clutches were laid in confinement on June 18 and July 1, and two others found under natural conditions and brought to the laboratory hatched on Sep-

tember 17 and 22. Neill and Boyles (1957:78) pointed out that this species, like the crowned snake, ovulates many more eggs than the two or three that constitute a normal clutch. Most of those in the oviducts of gravid females are small abortive eggs, which seemingly are resorbed.

Tantilla planiceps.—In the Big Bend region of Texas, Minton (1959:50) reported a gravid female of *T. p. atriceps* which contained a single egg ready to be laid on June 1. Stebbins (1954:452) reported that two females of *T. p. utahensis* collected in the Kingston Mountains of southeastern California each contained a single large egg.

Tantilla schistosa.—Stuart (1948:83) reported two juveniles that appeared to be not many days old on June 25, 1938, in Alta Verapaz, Guatemala.

Telescopus

These are slow-moving terrestrial snakes of Africa and southwestern Asia. FitzSimons (1962:186) stated that the African tiger snake, *T. semiannulatus,* lays a clutch of six to 10 eggs. In Nyasaland, Loveridge (1953:267) reported a gravid female with 14 large eggs on November 8 and another with 10 on January 24. In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman and Chapman (1962:427) found a female in May having 17 large (9 × 4 mm) ovarian follicles, and another in June having nine oviducal eggs. Perhaps there is some egg-laying throughout the year.

Thelotornis

The African bird snakes are oviparous and arboreal and have exceedingly elongate, slender and tapering bodies and tails. FitzSimons (1962:205) wrote that in southern Africa, six to 10 eggs are laid by *T. kirtlandii* about midsummer—December or January.

Trimorphodon

The lyre snakes are nocturnal and oviparous and occur in arid regions of the southwestern United States, Mexico and Central America. The records assembled below suggest that they do not conform to the seasonal pattern typical for Temperate Zone snakes, with mating in spring, egg-laying in early summer and hatching in late summer. In the San Antonio Zoo Werler (1951: 46) noticed vigorous courtship in a pair of *T. biscutatus* on November 2, 1948, and the female laid 20 eggs between December 29 and January 7. A female from Colima laid 20 eggs on March 3, 1949. Stebbins (1954:456) wrote that a clutch of 12 eggs was laid by a California lyre snake, *T. vandenburghi,* in September, and he mentioned another clutch that hatched after 79 days of incubation in the laboratory, and stated that a brood of apparently newly hatched young were found in the field on October 1.

Natricinae

This subfamily of colubrids including the water snakes and their near relatives was proposed and defined by Cope (1900:956) and

further defined by Malnate (1960). The North American natricines belong to nine genera and comprise a compact and well-defined group of viviparous snakes, whereas the Old World forms comprising many genera are all oviparous except for a single species, *Natrix annularis*. Many of the Old World species are tropical or subtropical in distribution.

Adelophis

The two small, rare, and secretive species occur in México and are closely related to snakes of the genera *Tropidoclonion* and *Thamnophis* according to Rossman and Blaney (1968). These authors stated that a female of *A. foxi* from Mil Diez, Durango, gave birth to two young and passed an infertile egg on August 3, 1966; a gravid female obtained from the same locality in 1967 gave birth to four young on July 29.

Amphiesma

This is a genus of small oviparous water snakes in southeastern Asia. Records indicate that the number of eggs in a clutch is small, usually not more than 10, and that in the tropical southern part of the range there is an extended breeding season, with the possibility of multiple clutches.

Amphiesma craspedogaster.—Pope (1935:106) reported five females of this southern Chinese species that contained 1, 5, 5, 5, and 7 eggs, and Malnate (1962:287) published additional records of two females with four eggs each and one with two. Gravid females recorded by Pope were collected between June 12 and July 20.

Amphiesma pryeri.—This is a species of the Riukiu Islands. Malnate and Munsterman (1960:54) reported females containing 2, 3, 3, 4, 5, and 6 eggs.

Amphiesma sauteri.—Malnate (1962:268) reported females containing 2, 3, 4, 5, and 5 eggs in southern China.

Amphiesma stolata.—The striped keelback is widely distributed in southern Asia. Smith (1943:305) stated that mating probably takes place "during aestivation" in the dry season, and that clutches of five to 10 eggs are laid from May to September. Wall (1921:113) recorded gravid females from April to October with the greatest number in July. Wall (1911:614) mentioned gravid females containing 5, 8, 11, and 14 eggs, and the finding of many gravid females from April to September. In West Pakistan, Minton (1966:137) reported that a female laid 10 eggs on May 21, and these began to hatch on June 7.

Amphiesma vibakari.—Fukada (1965:67) described the reproduction of this species in Japan. He observed courtship in captives on June 17, and observed "snake balls" in the field on May 17 and June 6. One ball consisted of a female and four males, the other of a female and six males. Egg-laying occurs in July or early August. In 10 clutches the average was 6.4 (4 to 10) eggs. Recorded incubation periods were 34 to 37 days.

Clonophis

This monotypic North American genus usually has been included with either *Natrix* or *Regina*. It is a near relative of the typical water snakes, genus *Natrix*, but is secretive and not aquatic in habits. Kirtland's water snake (*C. kirtlandi*) is a small, secretive species of Indiana, Ohio, and the adjacent parts of neighboring states. Conant (1938:77), Minton (1944), and Wright and Wright (1957:499) published data concerning number of young and time of birth. Litters contained 4, 5, 6, 6, 6, 7, 7, 7, 7, 7, 8, 8, 8, 8, 9, 11, 12, 22, 22, and 22 young (average 9.6). Births have been reported on September 7, 8, and 21.

Macropisthodon

This genus includes several oviparous Asiatic water snakes. The records indicate a long breeding season, at least in the southern, tropical part of the range.

Macropisthodon plumbicolor.—Wall (1921:130) reported one gravid female green keelback on February 16 and others in May and June. He reported that one laid 16 eggs, March 20 and 21, and that another laid seven eggs in late March and the first day of April.

Macropisthodon rudis.—Pope (1935:163) mentioned gravid females which contained 18, 22, 23, and 25 eggs. Two were collected between June 12 and July 20.

Natriciteres

This is a monotypic smooth-scaled water snake genus of tropical Africa. It is closely related to the more familiar *Natrix* and was long included in that genus. Like most of its Old World relatives, *N. olivacea* is oviparous. The records enumerated below seem to indicate that breeding occurs throughout much of the year but that there are local differences, and at times relatively few of the snakes or none of them are breeding. Doubtlessly the seasonal distribution of rainfall and its effect on the food supply determines the time of breeding in this kind of snake.

Natriciteres olivacea.—Loveridge (1936:237; 1958:34 and 40) published notes concerning the reproduction of the olive marsh snake in tropical East Africa. Females containing large eggs were reported at Kaimosi, February 14 and 19 and at Ngatana, June 11 to 20 (five specimens). A sixth individual from the last named locality had relatively small eggs. A female from Dar es Salaam laid eggs on June 15. The eggs in these clutches numbered 6, 6, 6, 6, 6, 6, 6, and 8 (average 6.25). All pertained to *N. o. olivacea*. In *N. o. uluguruensis* occurring at higher altitudes, clutches were smaller, with 2, 2, 3, 4, 4, and 4 eggs found in gravid females on the following dates: July 22, October 8, October 9, November 19, November 25, November 29, at Bagilo, Nyange and Amani. The specimen collected on October 8 had eggs only 5 mm in diameter, but others had large eggs nearly ready to be laid, 16 to 22 mm long and 6 to 8 mm in width. However, Loveridge noted that in November the majority of

females contained only minute ova. A long breeding season, extending over much of the year, is indicated.

Natrix

This large genus includes the typical water snakes of North America, Europe, and Asia. Many species formerly included under *Natrix* have been transferred to other genera, such as the North American *Clonophis* and *Regina,* the Asiatic *Amphiesma, Rhabdophis* and *Xenochrophis* (Malnate, 1960; Rossman, 1963), and the African *Natriciteres,* but those still included in the genus comprise a rather diverse lot. With a single exception, the European and Asiatic species are oviparous, resembling in this respect the many other Old World genera and species of the subfamily Natricinae. In contrast, the North American species of *Natrix* are viviparous, as are their New World relatives in eight other genera. Both oviparous and viviparous species are highly prolific. Correlated with the large number of young in a brood is the unusually small size of the young at birth or hatching. This in turn can be related to the piscivorous habits and the availability of fishes over a wide size range.

In north temperate climates there is a brief spring breeding season, but farther south available dates indicate that the breeding season is much more extended. In the extreme southern United States and to the southward the season of activity is sufficiently long to allow for two consecutive gestation periods, with the possibility that even a viviparous snake might produce young twice in a year, but no actual instances are on record for members of this genus.

Natrix annularis.—This South Chinese species differs from other Old World *Natrix* and their near relatives in being viviparous. Pope (1935:99) mentioned females that contained 4, 5, 6, 6, 9, and 9 eggs or embryos. In four others that he cited there were nine to 13 eggs and one that he found giving birth on September 28 had a litter that totalled 13 young.

Natrix cyclopion.—The green water snake is a large species of the southeastern United States. Seemingly, it is one of the most prolific snakes; females in Florida have been reported with the following numbers of embryos or young: 20, 20, 42, 67, 79, 97, 101 (Wright and Wright, 1957:473, 477; Betz, 1963b: 575; Duellman and Schwartz, 1958:307). Other recorded litters were much smaller, with 4, 9, 14, 16, and 19 young and too few records are available to indicate the usual or average number with any degree of accuracy. Courtship and mating activity has been observed in the first three weeks of April in Louisiana. Births of litters have been reported in mid-June and on June 19 and 21, on July 15, July 15, July 27, July 28, and August 7 in Florida, on July 16 and August 10 in Texas, and on September 20 in Missouri.

Natrix erythrogaster.—The red-bellied water snake and its subspecies are widespread in the southeastern United States and northeastern Mexico. Mating has been recorded on April 22 in Michigan and on June 16 in Illinois (Wright and Wright, 1957:482, 484). Dates for litters born in captivity are, for Illinois: September 4; for Missouri: September 15, 19, 20, 21 (2 litters), 22, and on October 2 (Anderson, 1965:136); for Texas: September 4. Seemingly as in many other Temperate Zone snakes, mating in spring, gestation in summer and birth in early autumn is the normal pattern for this species. Conant

(1965:144) mentioned a female of *N. e. alta* obtained near Rancho Grande, Zacatecas, México, in August 1960, which gave birth to 14 young on September 30, 1960. Kept in isolation she gave birth to another young and passed several infertile eggs nearly two years later on September 13, 1962. Excluding the last mentioned birth as somewhat abnormal, 20 litters averaged 16.0 young, and numbered 5, 8, 8, 11, 13, 13, 14, 14, 14, 15, 16, 16, 17, 18, 20, 22, 22, 22, 25, and 27.

Natrix fasciata.—Wright and Wright (1957:528, 536) stated that for the banded water snakes (*N. f. fasciata* and *N. f. pictiventris*) litters ranged from nine to 50, and they cited specific records of litters with 22, 23, 25, 29, 31, 33, and 57 young. For *N. f. pictiventris* of Florida, recorded birth dates are all relatively early—June 10, 21, and 28, July 10, 13, 16, 17 (two litters), and August 2. The salt marsh and mangrove water snakes, *N. f. clarki* and *N. f. compressicauda*, are distinct ecologically from the inland banded water snakes. They are relatively small and probably have smaller litters. Some published records are: 3, 4, 5, 6, 8, 11, 12, 14, 14, 15, 21 and 24 young, average 11.4. Swanson (1948:106) observed copulation in captives from Key West, Florida, in late January, and February 11 to 22. Wright and Wright (1957:517) mentioned a female from Texas that contained embryos in January. Births have been observed in *compressicauda* on June 13 and on July 23 and 28, and in *clarki* on July 27 (Bishop, 1940:128; Wright and Wright, 1957:517; Duellman and Schwartz, 1958:307).

Natrix maura.—Like most other Old World water snakes, this species of southwestern Europe is oviparous. Blackwell (1952:134) reported that one obtained in the Pyrenees Mountains laid 32 eggs while being transported in a travel case between July 24 and July 30. These eggs hatched between September 6 and 14.

Natrix natrix.—Smith (1951:229-233) described in detail the reproduction of this common British snake. Mating occurs occasionally in autumn but is most frequent in April and May. Egg-laying is in June and July. Often the clutch has 30 to 40 eggs, but the smallest productive females have only eight to ten, whereas a maximum of 53 has been recorded in a large female. Embryos have already begun their development at the time of egg-laying, and incubation requires approximately two months. Often there is communal egg-laying with many clutches deposited together. Manure heaps or other such media which generate heat are frequently chosen as the nest sites. Hatching is ordinarily in late August or early September, but there is a possibility that some young overwinter in the eggs. The male may mature by the autumn of the third year.

Fuhn and Vancea (1961:300) wrote that in Romania this snake mates in April or May, and egg-laying occurs in July or August.

Natrix rhombifera.—Betz (1963a) studied the ovarian cycle of the diamond-backed water snake with specimens from southeastern Missouri and La Place, Louisiana. In Missouri ovulation usually occurs between May 15 and June 15 and gestation is of approximately three months' duration. At the time of ovulation immature ovarian follicles of two successively smaller and distinct size groups can be discerned. Follicular growth is gradual over a two-year period, but in the spring of the third year the follicles enlarge rapidly. As the follicles mature, their numbers decrease, probably through atresia. In pregnant females

disparity between the total number of fetuses and number of corpora lutea can be accounted for by the numbers of dead embryos and yolk masses undergoing resorption. Counts of eggs in gravid females or of young born in captivity are available for 22 broods which averaged 47.3 (14 to 62, Anderson, 1965:138; Betz, 1963a:695; Guidry, 1953:53; Force, 1930:33; Cagle, 1937:184; Wright and Wright, 1957:502). This average may be high for the species, as the records include series of gravid females kept for study by Betz and by Cagle, and there may have been some selection in obtaining or keeping them. Nevertheless the records indicate that *N. rhombifera* is one of the most productive of snakes. Reported birth dates are August 5, 5, and 27; September 3, 7, 10, 10, 13, and 25; and October 2. Anderson mentioned a female which gave birth to six young on September 9, and gave birth to the remaining 24 young of her litter almost four weeks later on October 5. All the young were born alive and appeared to be normal.

The brown water snake, *N. taxispilota* is the geographical representative of *N. rhombifera* in the southeastern United States and perhaps the two should be considered conspecific; anyhow they are similar ecologically. In Florida, Franklin (1944:250) found 30 to 40 young in 30 broods. He found that the breeding season is usually during the latter part of May with young born in early August, but young may be born as early as June 15 or as late as late September. Duellman and Schwartz (1958:309) recorded a litter of 16 young.

Natrix sipedon.—Much literature concerning this species and its geographic races has been assembled and summarized by Wright and Wright (1957:511-551) from whose work the following figures are borrowed. Besides records from previously published literature those cited by the Wrights included some of their own and many from the unpublished dissertation of E. E. Brown. Seemingly mating occurs only in spring. For the northern subspecies, *N. s. sipedon*, litters of the following sizes are on record: 8, 9, 11, 14, 15, 16, 18, 19, 20, 21, 22, 23, 24, 25, 26, 27, 28, 29, 30, 37, 38, 39, 40, 41, 44, 45, 46, average 26.5 not including record litters of 99 and 76 (Slevin, 1951:132). Some of these figures appear repeatedly in the records. In certain cases it is difficult to determine which are original and which are repeated from older publications, but records are concentrated in the range 16 to 30. Birth dates reported for litters of the northern water snake are: August 9, 12, 15, 17, 18, 19, 20, 21, 22, 23, 24, 26, 29, 30, 31; September 3, 6, 8, 9, 11, 15, 23; and October 10 and 12. Obviously the latter half of August is the usual time for birth of litters, but with a few appearing earlier, and some much later. For *N. s. insularum* of Lake Erie births have been reported relatively late in the season: September 5, 25, and 26.

Natrix tessellata.—Fuhn and Vancea (1961:308) wrote that egg-laying of this species occurs in June and July in Romania.

Natrix trianguligera.—In Kopstein's (1938:164) study of Malayan snakes he reported a gravid female of this species in April, one in June and one in August. A long breeding season is indicated, and undoubtedly two or more clutches can be produced by a female during the course of a season.

Opisthotropis

These small, montane, Asiatic water snakes are oviparous; the average clutch of eggs is small. Pope (1935:170) collected gravid females of *O. kuatunensis* in Kuatun, China, between June 12 and July 20. There were five eggs in three, six in two, and three in one. Pope (1935:175) stated of *O. latouchii*: "The number of eggs ranges from 1 to 4. Thirteen preserved females contained 3 eggs, eight contained 2, while 4 eggs were found in only six. A single one held but 1 egg." In addition Pope was brought clutches numbering 2, 2, 3, 3, and 4; for the total of 33 clutches average was 2.84. In one instance the female was coiled about the eggs, seemingly guarding them. Eggs were found under flat rocks along swift mountain streams, and, in one instance at least, were partly submerged in water.

Pseudoxenodon

These Asiatic water snakes are oviparous. Pope (1935:154) mentioned a specimen of *P. macrops* taken in the Chin Hills in Burma on May 20 which contained six eggs. Taylor and Elbel (1958:1149) mentioned one captured in Thailand which contained ten ovarian eggs on January 19, 1958. The same authors mentioned a juvenile taken on June 14, 1954, which was 263 mm in length—probably near the size at hatching.

Regina

The North American striped water snakes of this genus have usually been placed under *Liodytes (alleni)* or under *Natrix (grahami* and *septemvittata)*, and probably they are derived from a *Natrix*-like ancestor. All are confined to the eastern half of the United States. All are viviparous. They differ from *Natrix* species in the same area in medium to small size, crayfish-eating habits, and relatively small litters of young. Rossman (1963) has redefined the genus.

Regina alleni.—Wright and Wright (1957:422) and Duellman and Schwartz (1958:313) mentioned the following numbers of young born, or eggs or embryos, in striped swamp snakes: 4, 6, 6, 6, 7, 8, 9, 9, 12, 34, average 10.1. They mentioned birth of young on June 24 (two litters) and in August, and the finding of a female containing embryos on March 20. The meager records imply a remarkably long breeding season. The mild climate and long growing season in the range of *R. alleni* possibly permit it to produce more than one litter per season.

Regina grahami.—Graham's water snake is a secretive, aquatic crayfish-eating species of the prairie region. In Texas, Curtis (1949b:9) observed three mating pairs on the night of May 9 and Anderson (1942:213 and 1965:125) recorded mating in Missouri on April 21 and May 10. Litters of the following sizes have been observed: 6, 8, 9, 10, 13, 14, 14, 25, 27, and 31, average 15.7. Birth has been noted July 29, August 15, and September 3, 5, and 10 (Smith, 1961:250; Wright and Wright, 1957:492; Anderson, 1942:213). Hall (1969: 159) examined 16 gravid females, and eggs or embryos averaged 18.6 (9 to 39). For the total of 26 litters the average was 17.4, but some of these were reported because they were considered exceptionally large.

Regina septemvittata.—The queen snake is a small striped water snake of forest streams in the eastern United States from the Great Lakes to the Gulf of Mexico. Information regarding the species' reproduction has been published by many authors. These records have been summarized by Wood (1949:749), Conant (1951:81, 233) and Wright and Wright (1957:508-509) and additional records have been published by Smith (1961:257). Eliminating duplications, 20 litters had: 5, 6, 6, 7, 8, 8, 9, 10, 10, 11, 11, 12, 12, 12, 12, 13, 14, 17, 18, and 23 young, average 11.2. Reported birth dates include: July 6 and 30, August 4, 5, 7, 10, 12, 18, 23, and 31, and September 5, 7, and 9.

Rhabdophis

These Asiatic water snakes occur in a variety of climates. They are oviparous, and in the tropics at least, there is year-round breeding, but with definite peaks and troughs determined by the amount of precipitation, and probably the food supply.

Rhabdophis chrysarga.—In Malaya Kopstein (1932:79) found that this species lays four to seven eggs most often in the period September to January, the rainy season, and the eggs require about two months' incubation. In Java DeHaas (1941:343, 347) found gravid females every month of the year but there were more than twice as many in the dry-season months, June through November, as in the remainder of the year. Adults made up from 70 to 90 per cent of each monthly sample from June to November, but through December, January and February the proportion of young steadily increased, until they outnumbered adults. In the spring months the proportion of young steadily decreased.

Rhabdophis himalayana.—Smith (1943:301) recorded a mating of the Himalayan keelback on July 24.

Rhabdophis nuchalis.—Pope (1935:111) recorded gravid females of this montane species of southwestern China collected on April 27, April 27, and May 17.

Rhabdophis subminiata.—This widely distributed species was studied along with other common snakes, by Kopstein (1938) in Malaya. He recorded three gravid females in July and four in August, one each in February, May, June, October and November. One female in captivity produced a clutch of eggs on June 28 and a second clutch 55 days later on August 21. Another produced a clutch on October 2 and a second clutch 44 days later on November 15. In west Java, DeHaas (1941:343) found gravid females every month of the year, but there were more than twice as many in the period June through November —the drier part of the year—than there were from December through May. In his August and September samples all snakes were adults but in succeeding months the young made up a progressively larger proportion till reaching a maximum of 87 per cent in March and then again decreased. In regions near the equator, as Malaya and Java, the species seemingly breeds throughout the year but with a pronounced peak and trough. Kopstein (1938:162) found that the male attains sexual maturity in only 13 months from the time of hatching, and the female in 17½ months.

Rhabdophis tigrina.—This medium-large water snake has been thoroughly studied in Japan by Fukada (1965:66) who has presented an excellent summary of the life history. Mating occurs chiefly in autumn (October to mid-November), but also in spring. Egg-laying occurs from late June to early August. Eighty-four egg-complements averaged 12.3 (2 to 26). However, the productivity tended to be proportional to the length of the females, as follows: 70 to 79 cm—8.3 eggs; 80 to 89 cm—10.9 eggs; 90 to 99 cm—14.2 eggs; 100 cm or larger—16.7 eggs. At room temperature incubation averages 37.6 (29 to 45) days. In both sexes breeding maturity is attained in autumn at an age of approximately one year and three months, and the smallest breeding females (620 mm) are only about half the maximum length. A clutch is produced annually.

Seminatrix

This monotypic genus of the southeastern United States is viviparous and probably is closely related to *Natrix*. In the mild climate where it occurs the breeding season is long. The seasonal cycle of the Florida black swamp snake, *S. pygaea*, was studied by Dowling (1950) with a series of 203 specimens. He found that ova enlarge in spring and that the young per litter are usually five or six with extremes from two to 11. Wright and Wright (1957:665) summarized literature records and listed the following counts of eggs found in females or young in litters born in captivity: 3, 5, 5, 7, 8, 9, 11, average 6.86. Birth dates mentioned include August 20 and 21, and October 18. The notable spread in dates suggests the possibility that a female might produce a second litter within one season, even though there is a gestation period of many weeks.

Storeria

Members of this genus are small, terrestrial, secretive, viviparous natricines. *S. occipitomaculata* is mainly confined to the eastern half of the United States and southeastern Canada, whereas *S. dekayi*, which is sympatric with it through much of this same area, occurs also southward into the tropics. In both species mating is known to occur both before and after hibernation. Most records of births are in late summer but in the southern part of its range *S. dekayi* may give birth in early summer and obviously has a much altered breeding schedule, perhaps with multiple broods.

Storeria dekayi.—De Kay's snake occurs under diverse climatic conditions. In a study at Flushing, Long Island, Clausen (1936:98-102) found that copulation occurred in the last week of March or early April. In eight instances the time between copulation and parturition was recorded in females kept in isolation after mating was observed. Supposed gestations ranged from 105 to 113 days and averaged 109.5, with parturition occurring from July 14 to August 1. Over the range as a whole there are notable deviations from this schedule, as copulation has been observed at various times of year. Minton (1944) recorded birth of a litter in Indiana on June 26, and in different parts of northeastern México, Taylor (1949:206) and Fouquette and Rossman (1963: 196) have reported full term fetuses on June 29 and June 30, respectively. Stuart (1948:63) reported a female "with well-formed eggs" on March 27 in Alta Verapaz, Guatemala. Later the same author (1954:59) reported a female

in Guatemala containing nine eggs on March 8 and he reported a juvenile only a few days old on May 27. Conant (1951:92) reported a female having large eggs in October, and Wright and Wright (1957:701) mentioned a female captured in November ". . . which laid eggs March 20." Presumably premature extrusion of embryos by a female kept active when she would have normally been hibernating was involved in this latter record. Other published birth dates listed by Wright and Wright include: July 6, 14, 18, 20, 21, 22, 24, 25, 26, 28, 28, 29, 30, 31, 31; August 1, 1, 3, 4, 8, 8, 11, 14, 14, 14, 16, and 17; and September 4 and 14. For 62 litters reported in the literature the average is 14.0 (3 to 27) with the majority of litters in the range 11 to 18.

Storeria occipitomaculata.—The red-bellied snake is widely distributed over the eastern half of the United States. Both fall and spring copulation are known to occur regularly (Trapido, 1940:107). Spermatozoa remain viable over winter in the female's oviduct so that a spring mating often is not necessary to effect fertilization of the eggs.

In Michigan Blanchard (1937:151) found a 1-1 sex ratio. He found that the snakes attain sexual maturity in their second year and become parents at an age of approximately two years. Most young were born between the 10th and 23rd of August but some appeared in late July and some as late as September 5. In 77 broods he found the number of young ranged from one to 13 and averaged 7.18. There is some indication of geographic variation in numbers of young. For 43 additional litters from localities well scattered over the geographic range (Wright and Wright, 1957:719; Smith, 1961:244; Denman and Lapper, 1964:28) there were, on the average, 9.35 (2 to 21) young (or ova or embryos in gravid females). In addition three females kept together gave birth to a combined group of 23 young which were not individually assignable to their separate litters. Recorded birth dates were: June 18 and 30; July 17, 19, and 24; August 22, 23, 28, and 29; and September 4, 5, 7, 7, 9, 10, 19, and 26.

Thamnophis

The garter snakes are the most abundant of North American snakes, occurring from the subarctic south into the tropics, with a large number of species and subspecies. All are viviparous. They are notoriously prolific. The usually large litter is correlated with small size of young at birth, but growth is remarkably rapid and sexual maturity may be attained in the second year. Size of litter is subject to much variation, both interspecifically and intraspecifically. Several population studies have indicated that varying percentages of the adult females may not become fecund in any one breeding season. Whereas various oviparous snakes are known to lay successive batches of eggs in the same season, the garter snakes are the only *viviparous* snakes definitely known to produce more than one litter in the course of a year. Such production is possible only in the extreme southern United States or regions to the southward, in a mild climate, with winter inactivity brief or lacking, and even under these conditions it may be exceptional.

Thamnophis butleri.—This small northeastern garter snake was studied by Wright and Wright (1957:818) and Conant (1938:98). The latter author mentioned two females that mated in captivity in the Toledo Zoo in different

years on March 23 and April 4, and gave birth to litters on July 3 and July 2, respectively. Other reported birth dates are July 28, August 4, and August 7. Litters of 4, 5, 8, 10, 12, 12, 14, and 16, average 10.1, young have been recorded. Carpenter (1952b:239) studying these and other garter snakes in Michigan, found that some two-year-old females may produce young, but that the majority were not fecund until the third year.

Thamnophis cyrtopsis.—This is a widespread Mexican and Central American species which enters the southwestern United States in Texas and Arizona. Sabath and Worthington (1959:32) mentioned a Texas female which gave birth to seven young on August 14. However, Minton (1959:49) wrote concerning his observations on this species in the Big Bend region ". . . on June 29, I collected two very small ones about 8 inches in total length and probably only a few days old. This suggests an autumn or winter breeding season." In the Guadalupe Mountains of southern New Mexico Mosauer (1932:16) noticed that about July 20 young, apparently newborn, appeared in large numbers along a canyon stream. Woodin (1950:39) reported birth of a litter of 25 young on June 15 in Arizona.

Thamnophis elegans.—This garter snake with its many geographic races is widespread in the western United States. It is remarkable in having diverged into an aquatic and a terrestrial series of subspecies. Their intergrading contact is in southern Oregon and northeastern California, but to the southward each group becomes increasingly specialized for its terrestrial or aquatic mode of life. In many areas the geographic representatives of these two main lines coexist without interbreeding. The isolating mechanism is not fully understood. Differences in habitat and in body size would in themselves reduce the incidence of interbreeding, but seemingly far more effective mechanisms are involved, preventing even occasional cross-breeding. Seasonal differences in sexual cycles might logically be suspected, but insofar as can be determined there are no such differences. Seemingly the snakes of all populations normally breed in spring and young are born in late July, August, or September (Fitch, 1940:113). Mating under natural conditions has been observed on March 16 and 21 and May 2 in terrestrial representatives and on April 13 and June 26 in the aquatic representatives.

Fox, Gordon and Fox (1961:60) reported the following numbers of young in litters of *T. e. terrestris* born in the laboratory: 6, 7, 9, 10, 10, 10, 11, 11, 11, 11, 15, and 16, average 10.6. A somewhat smaller average of 8.6 was noted by Stebbins (1954:416) for eleven litters. In the Puget Sound region Hebard (1950:217) mentioned 271 offspring of 28 broods of *T. e. vagrans*, an apparent average of 9.7, but since his observations were not concerned with litter-size as such, there may have been unmentioned escapes, discards, aborted or abnormal young that were not included. For the aquatic southern subspecies *T. e. hammondi*, Stebbins (1954:422) reported birth of a remarkably late litter of 25 young on October 30.

Thamnophis eques.—In Alta Verapaz, Guatemala, Stuart (1948:63) reported a gravid female (*T. e. fulvus*) containing nearly full-term embryos on May 17.

Thamnophis marcianus.—This is a species of desert watercourses in the southwestern United States and northern México. Relatively little has been

written concerning its reproduction. Wright and Wright (1957:804 and 806) and Stebbins (1954:428) have listed litters of 6, 9, 11, 12, 12, 16, 18, and 18, average 12.8 with birth dates of June 19, and July 5, 15, 21, 24, 30, and August 2.

Thamnophis ordinoides.—This snake was studied by Hebard (1951:177) in the Puget Sound region of western Washington. He found that copulation occurred in both fall and spring; abundant motile sperm were found in the oviducts of females examined from September 20 through October 9, and courtship activity was prominent from the March 27 first emergence through mid-April. Gravid females contained an average of 8.8 (3 to 15) embryos. However, in a series of 66 adult females 33 per cent were not gravid. Such individuals when dissected revealed pinkish ovarian scars that were thought to represent the previous year's corpora lutea.

Thamnophis proximus.—A population study of the western ribbon snake was made by Tinkle (1957:75, 76) in southeastern Louisiana. He found that from April through July 88 per cent of adult females were gravid. In 13 gravid females, number of ova were: 6, 9, 12, 12, 12, 13, 14, 14, 14, 14, 15, 17, 17, for an average of 13.0. Productivity was found to be closely correlated with the size of the female; the largest had 17 ova and the smallest only six. Tinkle stated, "Most snakes reached sexual maturity at an age of two years, but some were not mature until their third spring." Other records for various parts of the range were assembled by Wright and Wright (1957:830) and some for southern Oklahoma were published by Carpenter (1958:113). The combined data of these authors show litters of the following sizes: 4, 5, 6, 8, 8, 9, 9, 9, 9, 10, 12, 12, 12, 12, 14, 15, 15, 17, 18, 20, 27, average 12.0. Recorded birth dates include: July 4, 7, 18, 27, and 30; and August 9, 16, 20, 24, 25, and 31; and September 14.

Although best known from the central United States, the ribbon snake ranges far south along the Gulf Coast, into subtropical and tropical regions and in fact is the southernmost of all *Thamnophis*. Neill (1962:240) wrote that one captured in early April in British Honduras gave birth to six young on July 3. Conant (1965:140) obtained a pair from near Santa Catarina in Nuevo León, México, on May 12, 1954. In four years of captivity both made notable growth. Although never observed in copulation they presumably mated repeatedly, and the female gave birth to a series of litters, as follows: 8 on June 2, 1956; 10 on September 1, 1956; 10 on May 15, 1957; 9 on August 31, 1957; and 13 on May 28, 1958. Although the unnatural conditions of captivity undoubtedly had some effect on the breeding schedule of these snakes, the records are unique in demonstrating the potentiality for production of two litters per year in the tropics even in a viviparous species with a long gestation period.

Thamnophis radix.—The plains garter snake has been the subject of several intensive studies. In the Chicago region Pope (1944:208) observed that mating occurred between April 19 and May 24 but might also occur in autumn, and births were concentrated in the first week of August. Wright and Wright (1957:822) listed the following numbers of young in litters: 5, 13, 13, 17, 18, 19, 20, 21, 25, 27, 30, 35, 37, 40, 60, 92, average 29.2. Some reported dates of birth are: August 6 and 31 and September 7, 29, and 30.

Seibert and Hagen (1947:19) studied a local population of these snakes in

the Chicago area through an entire growing season. They found distinct annual age-groups all of which showed increasing size as the summer progressed, but by far the greatest gains were made by the first-year snakes. Of those captured, 52.7 per cent were first-year individuals, 34.6 per cent were second-year and 12.6 per cent were third-year. The second- and third-year snakes were found to be reproductive, but no figures concerning the incidence of fecundity were presented.

Thamnophis sauritus.—Carpenter (1952a, 1952b) studied the ecology of the eastern ribbon snake in southern Michigan. He found an average of 10 eggs per female, and found that two-year-old females may produce young, but found it ". . . probable that many individuals of both sexes of the three species [*T. sauritus, T. sirtalis,* and *T. butleri*] do not reach mature size until approximately their third spring after birth." Wright and Wright (1957:826) listed litters (ova, embryos, or young born) of the following numbers: 3, 4, 4, 4, 4, 5, 5, 5, 5, 5, 6, 6, 6, 6, 8, 8, 9, 9, 9, 9, 10, 11, 11, 12, 12, 12, 12, 12, 12, 12, 14, 14, 14, 15, 16, and 20, average 9.1. Young were born on the following dates: July 23; August 1, 6, 7, 10, 10, 11, 12, 17, 19, and 26.

Neill (1962:241) reported that a large captive female from Richmond County, Georgia, produced a brood in July and another in early November, and a Florida female was also reported to have produced two litters in a season, but young of the second litter were dead and malformed.

Thamnophis sirtalis.—In a recent publication, I (Fitch, 1965) summarized the literature regarding reproduction in this widespread North American species which occurs from the subarctic southward through most of the United States. Mating may occur either in the fall or in spring but is especially concentrated in the first few warm days after spring emergence, which may be in late March or as late as early May, depending on latitude, altitude, and the trend of the weather. Ova are still small at the time mating occurs and several weeks pass before they have matured and ovulation takes place. In northeastern Kansas this is typically about mid-May, more than a month after emergence from hibernation. In a series of 132 gravid females from eastern Kansas eggs or embryos averaged 14.5 ± .031. The range was from seven to 20, but the average increased from 12.0 in two-year-olds to 16.8 in four-year-olds. For two-, three-, four-, five-, and six-year-olds the percentages of gravid individuals were, respectively, 42, 58, 93.5, 83, and 100.

In series from other parts of the geographic range somewhat different figures have been obtained. In Michigan, Carpenter (1952a:253) found an average of 18 young in 20 litters and in New Hampshire, Zehr (1962:324) found an average of 12.9 embryos in 104 gravid females. Occasional litters are much larger; there are seemingly authentic records of litters with 53, 64, 72, 74, 78, 80, and 85 young (Mattlin, 1948:149; Martof, 1954:100; Wright and Wright, 1957:840-841). For 100 other miscellaneous records of broods born in captivity, or embryos found in gravid females dissected, over the range as a whole, the average is 26. One possible explanation for the fact that this average so greatly exceeds those of the series examined by Carpenter, Fitch, and Zehr is that herpetologists have been somewhat selective in reporting unusually large litters and in keeping the largest gravid females in anticipation of the birth of their litters.

Over the range as a whole, the breeding cycle seems to conform closely to the same schedule, with ovulation in late spring, pregnancy in early summer and birth of young some time in July or August, but with minor differences resulting from latitude, altitude, and weather. Birth has been recorded as early as June 24 in southern Louisiana (Meade, 1934:4), and July 3 in Ohio but as late as October 9 in Ontario in the northeastern part of the range. "Two published records deviate notably from the normal timing of the breeding cycle: Barton (1952:198) reported a female of record size from Florida (received from Ross Allen's Reptile Institute) which produced a litter on May 31, 1952, and Triplehorn (1955:248) reported a female from Broward County, southern Florida, which produced a litter on January 11, 1952. Seemingly in the semi-tropical climate of southern Florida, the breeding cycle which prevails throughout temperate North America may be much altered because a well-defined season of winter dormancy is lacking" (Fitch, 1965:527).

Tropidoclonion

The lined snake of the central United States in the prairie region resembles a diminutive garter snake. It is a close relative of *Thamnophis* and perhaps derived from that genus but is terrestrial and secretive rather than aquatic in habits. Its resemblance to *Thamnophis* extends to its reproductive habits; it is viviparous, and mates either before or after hibernation. As in most diminutive snakes, litters are small and young are relatively large at birth.

Tropidoclonion lineatum.—Force (1930, 1931, 1936) and Ramsey (1946, 1953) have studied its habits and Wright and Wright (1957:882) have summarized miscellaneous notes regarding it. Litters have been reported with the following numbers of young: 2, 3, 4, 6, 6, 7, 8, 8, 9, 9, 9, 10, 12, average 7.15. In Oklahoma, Force found that births occur between the ninth and 31st of August. Ramsey observed birth of two litters on August 14. He observed mating in a captive pair on September 1. Curtis (1949:11) observed mating in October. Blanchard and Force (1930:96) found that sexual maturity is attained in the second year of life.

Virginia

The two diminutive and secretive natricines of this genus occur in unglaciated areas of the eastern United States. Both are viviparous and conform to a breeding schedule typical of snakes in the Temperate Zone, with mating in spring and birth of young in late summer or early autumn. Compared with the presumably ancestral *Natrix*, earth snakes have small litters of young, and the young are relatively large at birth.

Virginia striatula.—Wright and Wright (1957:289), Carpenter (1958:114), and Sabath and Worthington (1959:32) have published information regarding sizes of litters and time of their birth in rough earth snakes. Seventeen litters averaged 5.24 and had the following numbers of young: 2, 3, 3, 3, 4, 5, 5, 5, 6, 6, 6, 6, 6, 7, 7, 7, 8. Births of litters have been recorded on June 20 and July 4, 6, 8, 17, and 29, and August 13 and 20. Clark (1964:293) studied a local population of these snakes at College Station, Texas. He found that mating occurred in March and April, ovulation in May and June, and parturition

mostly from mid-July to mid-September. Number of young in 16 litters averaged 4.94 ± .48 (3 to 8), with positive correlation between number of young per litter and body length of female.

Virginia valeriae.—A few records of reproduction in the smooth earth snake have been published (Wright and Wright, 1957:291, 295; Smith, 1961:239). Numbers of young reported in litters were: 2, 2, 4, 4, 5, 5, 6, 6, 6, 6, 7, 7, 7, 7, 8, 8, 8, 10, 12, 12, average 6.6. In western Pennsylvania Bothner and Moore (1964:709) reported nine litters which averaged 6.8 (5 to 9) young. All young were born in September, from the 7th to the 30th. In Missouri Anderson (1965: 179) reported births on August 16.

Xenochrophis

These abundant Asiatic water snakes are like most other Old World natricines in being oviparous. They are noteworthy for the large number of eggs produced, and, at least in the tropical portion of the range, for the extended breeding season, with repeated layings by an individual female in the course of a year. In the literature *X. piscator* and *X. vittata* have usually been referred either to *Natrix* or to *Fowlea.*

Xenochrophis cerasogaster.—Malnate and Minton (1965:31) cited a personal communication from J. A. Anderson stating that two female dark-bellied marsh snakes from West Pakistan each laid 20 eggs in the first week of April, and they mentioned one young near hatching size collected in May and several collected in August. They suggested that hatching might occur at the onset of the rainy season which is usually in June or July. However, the meager records suggest that the breeding season extends over several months, and that like its more southern relatives, *X. cerasogaster* may produce more than one clutch in a season.

Xenochrophis piscator.—Pope (1935:122-123) summarized much published literature concerning the checkered keelback and added new information. The species is widely distributed in southern Asia and the Malay Archipelago. In Assam in northeastern India gravid females have been noted in December, January, February, April and May and elsewhere in India from May to November, inclusive. Seemingly breeding occurs throughout much of the year. This is one of the most prolific snakes; clutches of 8 to 88 eggs have been recorded. Wall (1907:870) reported 19 clutches with 20, 20, 21, 24, 24, 24, 24, 34, 36, 39, 41, 44, 47, 51, 53, 57, 57, 61, and 85 eggs, average 40. An incubation period of approximately 87 days is on record. In West Pakistan, Minton (1966: 136) reported the capture of several gravid females in February. Seven of these laid clutches of 34 to 75 eggs between March 8 and 29.

Xenochrophis vittata.—This was one of the common Malayan snakes studied by Kopstein (1938:163-164). He found gravid females in every month of the year, but there were three to five records each month from December (inclusive) through May (the rainy season) and only one or two records per month for the remainder of the year which included the dry season. One female kept in isolation produced a clutch of eight fertile eggs on March 26 and another clutch with the same number 41 days later on May 3. A second female produced successive clutches of five and six eggs on May 31 and Sep-

tember 27. Both sexes were found to require only 10½ months to attain sexual maturity. Early maturity, year-round breeding, and oviparity, with frequent clutches, combine to confer a remarkably high reproductive potential upon this tropical snake.

Xenodontinae

This subfamily, recently re-established through the findings of Smith (1963:288), Rossman (1966) and Underwood (1967), includes three or more genera of terrestrial, heavy-bodied, viperlike (though harmless), bufophagous New World snakes. They are oviparous.

Heterodon

This genus of three species occurs in the United States and northern México. In south-central Kansas, Platt (1969) ascertained the following facts concerning the reproduction of *H. nasicus*: less than half the adult females are gravid in any one breeding season and individual histories provide limited evidence of breeding in alternate years; most females produce their first clutches when they are 20 to 22 months old; in central Kansas most egg-laying occurs from July 2 to July 22, but records from elsewhere vary from June 3 to August 24. There are four to 23 (average 9.4) eggs per clutch but the clutch size is correlated with the snout-vent length of the female as follows: 490 mm or more, average 14.0 eggs; 440 to 489 mm, average 6.8 eggs; 439 mm or less, average 5.1 eggs. The recorded incubation periods are 52 to 64 (average 57) days.

In the same area in *H. platyrhinos* Platt found evidence of autumn mating (sperm in cloaca of a female on October 9) although spring mating is probably more frequent. He found four to 61 (average 22) eggs in 53 clutches. Most egg-laying in nature is in late June and early July, but the records span a much wider range in dates, from May 27 (Texas) to August 28 (Indiana). The wide range of egg-laying dates suggest the possibility that certain females produce second clutches but no instance of this has yet been recorded. Probably one clutch per year is the general rule. One marked female is known to have produced a clutch in 1962 and another in 1963.

Lystrophis

This South American genus contains three species, which occur mainly south of the tropics. Orejas-Miranda (1966:202) stated that the breeding season of *L. dorbignyi* is the southern spring and perhaps also early summer. Copulation was observed in September. Gravid females and egg-laying have been reported in November and December. Clutches of seven to 15 eggs have been reported. Hatching is mainly in January and February.

Xenodon

These frog-eating snakes of tropical South America seem to be near relatives of the North American hog-nosed snakes and resemble them in many ways.

Information is available only for *X. severus* which seems to have year-round breeding in the tropical equatorial lowlands. A series of these snakes in the American Museum's Bassler Collection from Iquitos, Perú, was examined by the writer, to determine the species' breeding cycle in that equatorial region. The population structure seemed much different than in most other kinds of snakes from the same region that were examined, with a remarkably large proportion of young, of all sizes from hatchlings to adolescents. Obviously, the reproductive potential is high. Only one gravid female was found; that one was collected in March, and contained 19 ova. Young that were near hatchling size—171 to 205 mm—and could not have been more than a few weeks old, were taken in the following months: January (2), March (2), April (2), September (1), November (1), and December (1). The well-dispersed seasonal distribution of these hatchlings provides evidence of year-round breeding in Iquitos.

Dipsadinae

This is a subfamily of Neotropical snakes having only three genera, and sometimes separated from the colubrids. As a group they show specialization for a diet of snails and slugs, and some are highly arboreal, with remarkably attenuate bodies and tails. The Asiatic counterparts are considered to belong to a different subfamily.

I examined series of the South American *Dipsas catesbyi* from Iquitos, equatorial Perú, in the Bassler collection of the American Museum of Natural History. Of five gravid females for which dates of collection had been recorded, one was taken in February, one in March, two in April, and one in September. A juvenile of 159 mm snout-vent was collected in June, and others of 187 and 172 mm were from September and October—further indication of an extended breeding season. Including many undated specimens, there were in all 28 gravid females and these averaged 2.7 ova; 12 had 2, 12 had 3, and there was one each with 1, 4, 5 and 6.

John D. Lynch observed the montane species *Dipsas oreas* at Tandapi, 1460 meters, Pichincha Province, on the Pacific slope of Ecuador, and he kindly provided the following notes. Nine young collected in late July of 1967 and 1968 were still near hatching size, with the following snout-vent lengths: 167, 192, 193, 203, 203, 210, 214, 216 and 217 mm. A female of 690 mm snout-vent length collected on July 22 contained seven eggs of about 28 × 15 mm. A clutch of four eggs was found on July 15, 1967 beneath a log in a pasture. They hatched on July 27, 1968. A long breeding season is indicated, because the young found in July must have come from eggs laid not later than early May. Perhaps there is some breeding throughout the year.

The Neotropical genus *Sibon* has been considered annectant between other dipsadines and colubrines. In northern El Petén, Guatemala, Stuart (1958:28) found a pair of *S. nebulata* together in late February, and from mid-March to mid-April he collected a series of a dozen juveniles "not many days old." In the Cayo District of British Honduras, Neill (1962:239) obtained a hatchling of *S. sanniola* which still had a prominent umbilical scar on November 1.

Pareatinae

These are elongate, arboreal, blunt-headed, tropical Old World snakes which resemble in appearance and habits the Dipsadinae of the American tropics, and perhaps are closely related to them. The genus *Pareas* has several species in southeastern Asia. In Malaya, Kopstein (1938:162) found that both sexes of *P. carinatus* mature within 11 months of the time of hatching, hence the length of generation is remarkably short.

Xenoderminae

This is a small group of colubrids occurring in southeastern Asia and neighboring islands and in Central America. They are peculiar in having body scales that lack free edges and are separated by areas of naked skin. The genus *Achalinus* has several species of small, secretive, earthworm-eating snakes in southeastern Asia. Fukada (1965:71) reported a female *Achalinus spinalis* from Japan that had four oviducal eggs of somewhat different sizes. Pope (1935:186) mentioned a female from southern Szechwan, China, that contained seven well developed eggs with small embryos, and another collected in "April or May" that contained four eggs ready to be laid. Maslin (1950:427) recorded a female from Kiangsi that contained six unlaid eggs on June 28. *Xenodermus javanicus* is a frog-eating species of the Malay Peninsula and neighboring islands; it frequents rice fields. Smith (1943:125) stated that from two to four eggs are laid at a time, but Taylor (1965:692) stated that it is ovoviviparous.

Homalopsinae

This is a subfamily of venomous, rear-fanged aquatic colubrids found in rivers and estuaries and along coast lines of tropical southern Asia and neighboring island groups southward to Australia. All are viviparous.

Cerberus

These are medium-small, fish-eating snakes of coastal habitats from Ceylon along the coasts of southeastern Asia and the Indo-Australian Archipelago. Wall (1921:259) reported gravid females of *C. rhynchops* in February (1), late March (3), and April (1).

Enhydris

These are stout-bodied, fish-eating snakes.

Enhydris chinensis.—Pope (1935:313) wrote that 17 females from Fukien, China, contained from three to 13 embryos and averaged 5.7. He mentioned additional unborn litters of 3, 6, 7, 8, and 13 young. One female with nearly full term embryos was captured on July 30 and another gave birth on August 27. Other gravid individuals were recorded in May and June and ". . . the birth season there [Futsieng Hsien] was nearly over by early September."

Enhydris enhydris.—Pope (1935:315) summarized several published records regarding the reproduction of this thoroughly aquatic and widely distributed snake. One female, taken near Rangoon, Burma, in March contained six ova. Another gave birth to 11 young. One from Bangkok, Thailand, had 10 small embryos in December; another had 18 large embryos in April and a third caught in July gave birth to a single dead young, probably the last of a litter. Taylor (1965:914) recorded 11 young born July 8, 1959, in Thailand. The scattered dates in this small sample indicate a long breeding season.

Enhydris plumbea.—Pope (1935:317) summarized information on the reproduction of this species. He stated that from two to 11 young are born (average about six), that females are gravid in May and that by late August the birth season is over, in Yenping and Hainan, China. However, Taylor and Elbel (1958:1159) recorded a female with 14 enlarged ovarian eggs in Thailand on November 28, 1954.

Homalopsis

This is a monotypic genus of Oriental water snakes.

Homalopsis buccata.—Berry and Lim (1967:310-312) studied the reproductive cycle of the puff-faced water snake in the equatorial climate of Kuala Lumpur, Malaya. Population samplings indicated that spermatogenesis is continuous throughout the year, and females with eggs or embryos were obtained in each bimonthly sample. In October-November, December-January, and February-March samples, reproductive females (with enlarged ovarian follicles or embryos) comprised between 85 and 90 per cent, whereas the percentage declined to 58.8 in April-May, 40.0 in June-July, and 50.0 in August-September. Fat bodies were found to be large in all adult females, but there was no evident correlation with state of ovary or oviducts, with eggs or embryos. In all, 43 reproductive females were examined, and litters averaged 9.26 (2 to 20).

Sibynophiinae

This small group of colubrids has representatives in Madagascar, Central America, and southeastern Asia. The small elongate,

terrestrial snakes of the genus *Sibynophis* occur in southeastern Asia and parts of Borneo, Java and the Philippines. Pope (1935:85) reported collecting two gravid females of *S. chinensis* in the Yenping mountains of China between April 12 and June 2, and at Kuatan on August 22 he was brought three eggs which contained embryos that were still small. Four preserved females contained two to four eggs each. Pope (1935:88) mentioned two gravid females of *S. collaris* collected in the Kachin Hills on June 6.

Dasypeltinae

This subfamily consists of medium-sized, egg-eating colubrids of India and Africa. *Dasypeltis scabra* is the widely distributed African egg-eater. Schmidt (1923:100) mentioned a large female distended with eggs in November in the Belgian Congo. In East Africa, Loveridge (1936:257; 1942:282) reported a female having numerous large eggs on December 23 and another with 14 eggs on January 16; he reported a female which contained six large eggs on April 21. A litter of young that probably were recently hatched, were collected on May 18. Gans, Laurent and Pandit (1965:68) reported a clutch of three eggs laid on September 25, 1961, by a female from the Somali Republic. These eggs hatched on the following January 11 and 12. The same authors mentioned other clutches of 8, 10, and 11 eggs laid by egg-eating snakes. From the distribution of dates in these records it seems that the breeding season is long and/or variable.

Elapidae

The elapids, including the cobras, kraits, coral snakes and their relatives are a family of front-fanged venomous snakes including many of those that are most feared by man and are important as destroyers of human life. Members of this family closely resemble colubrines in most respects, except for their highly developed venom glands, and tubular fangs for its injection. Elapids occur in both the Old World and the New World, and are found chiefly in the tropics and subtropics. The African spitting cobra, *Haemachatus,* is viviparous, as are most of the Australian genera (see Table 8), but the American and Asiatic elapids are all oviparous.

Cogger (1967:90) stated: "In the southern parts of Australia, the breeding season usually extends from about mid-October to the end of December. At least some specimens, though it is not known

Table 7. Incidence of Gravid Females from Month to Month in Year-round Collections of Snakes from Iquitos, Equatorial Peru (Bassler Collection, American Museum of Natural History). In Each Fractional Number the Numerator Represents the Gravid Females and the Denominator Represents all Females of Mature Size. Year-round Breeding is Suggested for those Species for which Sufficient Material is Available.

	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Oxyrhopus melanogenys	1/1	—	3/5	—	—	1/2	—	—	1/1	—	1/1	—
Dipsas catesbyi	0/2	1/1	1/1	2/2	0/1	0/1	—	0/1	1/3	0/1	0/2	—
Drymoluber dichrous	0/1	—	—	—	—	—	—	2/2	—	—	—	—
Imantodes cenchoa	1/1	0/1	—	—	—	—	0/2	—	—	—	—	—
Leimadophis reginae	0/1	3/5	7/14	0/1	—	1/3	—	2/9	1/2	—	1/2	2/2
Leptodeira annulata	3/5	1/3	4/8	—	0/2	1/1	—	3/8	1/2	1/4	1/3	1/2
Leptophis ahaetulla°	1/1	3/6	7/13	0/1	2/2	2/4	1/1	1/6	—	—	3/5	2/3
Leimadophis taeniurus	0/1	—	2/3	0/2	0/1	1/3	—	0/1	1/1	—	—	3/3
Oxyrhopus petolus	—	—	1/1	—	—	0/1	—	—	1/1	—	1/1	—

° Data for this species from Oliver (1947:5), who used the name *Thalerophis richardi*.

what proportion of the population, produce two batches of eggs or young, usually two months or more apart, and typically in January or March. This difference in time between the breeding or mating season and the hatching or laying season reflects the average time it takes for eggs to hatch after being laid, or the length of the gestation period in live-bearing species—about eight weeks." Cogger stated that in northern Australia most species lack a definite breeding season.

Table 8. Reproduction in Australian Elapids.*

Species	Mode of reproduction	Number of eggs or young
Acanthophis antarcticus	viviparous	9 to 15
Cacophis kreffti	oviparous	2 or 3
Cryptophis nigrescens	viviparous	----------
Demansia psammophis	oviparous	about 6
Demansia olivacea	oviparous	about 8
Demansia ornaticeps	oviparous	3 to 4
Denisonia maculata	viviparous	about 8
Drepanodontis daemelii	viviparous	6 to 12
Drysdalia coronata	viviparous	10 to 15
Drysdalia coronoides	viviparous	6 to 12
Drysdalia mastersii	viviparous	5
Glyphodon harriettae	viviparous	about 4
Hoplocephalus bungaroides	viviparous	about 8
Oxyuranus scutellatus	oviparous	10 to 20
Pseudechis australis	viviparous	----------
Pseudechis colletti	viviparous	12 or more
Suta suta	viviparous	about 6
Tropidechis carinatus	viviparous	----------
Vermicella annulata	oviparous	----------

* Based on statements by Worrell, 1964.

Austrelaps

This genus includes the Australian "copperhead" and swamp snake, characterized by having a small head hardly distinct from the neck and a venom powerfully neurotoxic and hemotoxic. The snakes live in swampy places and are viviparous. According to Waite (1929:219) the copperhead, *A. superba*, gives birth to from 10 to 40 young in summer (December or January) in South Australia. Worrell (1964:111) stated that there are usually 18 to 21 young.

Bungarus

This genus includes the kraits, nocturnal, burrowing and secretive elapids with polished scales, found from India to southern China, Malaya and Celebes. They are oviparous. Females are rarely found while gravid but are known to

remain and guard their eggs after oviposition. Wall (1921:443) mentioned clutches of eggs of the Indian krait, *B. caeruleus*, found in May (one) and June (two). Smith (1943:409) wrote regarding *Bungarus ceylonicus* that these kraits ". . . retire about September to mate and do not dissolve their matrimonial relationship until the young are launched upon the world in March." Wall (1921:453) mentioned a clutch of eggs found in January.

Callophis

The Oriental coral snakes are nocturnal, secretive and burrowing elapids closely related to the kraits. They occur from India to the Philippine Islands and Japan. Pope (1935:343) cited instances of gravid females of *C. macclellandi* with enlarged eggs, taken between June 12 and July 20, on August 6, and on August 8. There were 4, 6, and 14 eggs.

Demansia

This genus includes several slender, active Australian elapids known as whip snakes. Worrell (1964:118) wrote that the female black whip snake, *D. olivacea*, produces about eight eggs each summer.

Dendroaspis

The mambas are large, elongate slender elapids, with narrow heads and few scale rows. They are of terrestrial and partly arboreal habits. The group is entirely African and confined to regions south of the Sahara. These snakes are oviparous. In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman and Chapman (1962:430) reported a pair of *D. polylepis* copulating in June and a female containing ova 8 mm long in October. FitzSimons (1962: 311) stated that in southern Africa the usual clutch is 12 to 14 eggs, but occasionally there are only nine or 10.

Elaps

This genus of two species comprises the so-called dwarf garter snakes of Africa. They are longitudinally striped somewhat like the American natricine *Thamnophis*, but have small heads, cylindrical bodies, and scales smooth in only 15 rows. FitzSimons (1962:285) stated that in southern Africa, *E. lacteus* lays up to six eggs, in December or January.

Haemachatus

This is a monotypic genus of cobras endemic to South Africa and represented by the much feared ringhals, or spitting cobra. Isemonger (1962:72) stated that the ringhals *(H. haemachates)* gives birth to its young—unlike the other cobras, all of which are egg-layers. FitzSimons (1919:184) published a photograph of a female with her newborn litter of 28 young. FitzSimons (1962: 290) wrote that litters average between 20 and 30 young (sometimes as few as 15 or as many as 60) and that they are born in late summer—January to March.

Micruroides

This is a monotypic genus of southern Arizona and adjacent México, differing from the typical coral snakes in small size and more primitive dentition. Funk (1964:219) wrote that a Sonoran coral snake, *M. euryxanthus*, 416 mm in length contained two thin-shelled oviducal eggs on July 27, 1961.

Micrurus

The coral snakes are mainly a Neotropical group, but with one species in the southeastern United States. They are mostly medium-sized, brightly patterned, secretive, reptile-eating elapids.

Micrurus corallinus.—Mole (1924:258) wrote that on Trinidad this species has been seen mating in January, and that one was found with two eggs in July.

Micrurus diastema.—In Alta Verapaz, Guatemala, Stuart (1948:85) mentioned collecting a female of the many-ringed coral snake that contained well-formed eggs on April 4, 1938. In British Honduras, Neill (1962:241) obtained one 268 mm in length and having an indistinct umbilical groove on July 14. "The snake had probably seen about 5½ months of activity; and if it had gone through no inactive period, it might have hatched in late January or early February. Alternatively it could have hatched in late October or early November of the previous year, entering soon into a period of inactivity. . . ."

Micrurus elegans.—Stuart mentioned a Guatemalan female that had four well-formed eggs on May 21, 1940.

Micrurus fulvius.—Sabath and Worthington (1959:32) mentioned a large female Texas coral snake that contained seven eggs on May 5, 1956. Telford (1955:258) mentioned one in Florida that laid seven eggs on June 18, 1953, a week after capture. Werler (1951:46) mentioned a female from San Antonio, Texas, that mated at the Zoo on May 16 and 18 soon after capture and died on June 3 containing nine eggs almost ready to be laid.

Micrurus psyches.—Beebe (1946:47) wrote that on June 22 one collected in Kartabo, British Guiana, contained two large (25 × 7 mm) eggs still lacking shells.

Naja

The typical cobras are highly venomous, much feared, oviparous elapids occurring in southern Asia, Malaysia and much of Africa. They are medium-sized to large, active, terrestrial snakes.

Naja haje.—The Egyptian cobra is widely distributed in Africa. On the basis of observations made in the southern part of the continent, FitzSimons (1962:296) stated that the clutch consists of eight to 20 eggs.

Naja melanoleuca.—Wilson (1959:159) received six black and white cobras sent from Blantyre, Nyasaland, to him in Edinburgh, Scotland, in the summer of 1951. On November 23, 1955, a clutch of 17 eggs was laid by one female and two of these hatched the following February 9. Twenty-six eggs were laid

by one female on June 30, 1957. On April 16, 1958, a pair was observed courting; on May 12, 25 eggs were laid by a female thought to have been the same. At Kaimosi in East Africa, Loveridge (1936:272) noted that a female contained 15 eggs ready to be laid. Menzies (1966:175) reported a clutch of 26 eggs in Sierra Leone. According to FitzSimons (1962:301) there are usually about 15 eggs per clutch.

Naja naja.—Smith (1943:435) stated that in India pairing is in January and February and egg-laying is mostly in May but may extend over several months. He believed that ". . . from the time of pairing until the young are born [*sic*] the pair remain together and the male also takes a share in guarding the eggs. Incubation takes from 69-84 days." Also in India, Wall (1921:474) wrote that April and May were the principal months of egg-laying. He recorded a gravid female in January, several in February, and several in July and August. In Malaya, Kopstein (1938:164) found that like other "rice field snakes" the cobra did most of its egg-laying in the winter rainy season. He stated that the female remains with the eggs throughout the 88 days of incubation. In West Pakistan, Minton (1966:155) noted that young cobras appear in the last week of June and early July. Bogdanov (1966) studied the northern banded form *(N. n. oxiana)* in the temperate climate of central Asia. In that region cobras emerge from hibernation in March, and eggs are laid in July, with only one clutch of 9 to 12 eggs per year.

Naja nigricollis.—In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman and Chapman (1962:430) recorded a female that contained partly developed ova (10 × 5 mm) in June. There were 22 on the left side and 28 on the right. According to FitzSimons (1962:305) there are 10 to 22 eggs per clutch.

Notechis

In the Australian tiger snakes the general appearance is somewhat viper-like, as the body is moderately stout, and the head is broad and distinct from the neck. The snakes are viviparous and unusually prolific. Waite (1929:228) stated that the usual litter of *N. scutatus* is about 30 young but there may be as few as 17 or as many as 72, and in one instance 109 embryos were counted.

Ophiophagus

This monotypic genus includes only the king cobra or hamadryad, a giant elapid snake of reptile-eating habits, occurring throughout much of southeastern Asia and on neighboring islands. Smith (1943:438) mentioned the finding of two mating pairs of *O. hannah* at Palaw, Burma, in January and the finding of nests containing eggs in April, May and June. The female king cobra is known to guard her eggs throughout incubation, and accumulates a "nest" of plant debris in which they are kept. Oliver (1956) made detailed observations on a pair from near Bangkok, Thailand, kept at the New York Zoological Park. In 1955 three matings were observed, all in March within a period of nine days (but possibly there were other unobserved matings). In 1956 the same pair was observed mating on six occasions over a period of approximately 60 days. In *both years* the female started building her nest on April 20 and

laid her eggs on April 24. There were 41 eggs the first year and 51 the second. Young hatched 10 to 11 weeks after the eggs were laid.

Oxyuranus

This monotypic genus includes only the taipan, a formidable giant elapid of tropical northern Australia. Worrell (1964:89) wrote that the mating of Australian elapids, including *O. scutellatus*, takes place mainly after emergence from hibernation, in September and October. He mentioned "the spectacular wrestling of the males. . ." of black snakes, brown snakes and taipans, which occurs in the breeding season and continues "throughout each day for about a month." He stated that the taipan is oviparous, producing 10 to 20 eggs which hatch in 10 to 14 weeks. Loveridge (1945:157) mentioned one taipan that contained three oviducal eggs, and another that laid seven eggs between September 27 and October 6.

Pseudechis

This genus includes the Australian black snake and its near relatives, moderately large, slender, and active, viviparous snakes. Waite (1929:215) stated that for the black snake, *P. porphyriacus*, in South Australia, February and March are the usual birth months, and that there are usually from 15 to 20 young in a litter but there may be as many as 40. Worrell (1964:136) stated that there are usually 12 or more young in a litter.

Pseudonaja

This genus includes the several species of brown snakes that occur over much of Australia and part of New Guinea. The size range of the species is from small to large. Worrell (1964:139) wrote that mating of the Australian brown snake, *P. textilis*, takes place in October and November and the female lays 20 to 30 eggs in December or January.

Walterinnesia

This is the genus of the desert cobra in North Africa and southwestern Asia. Anderson (1963:471) mentioned an Egyptian cobra, *W. aegyptica*, from Iran that had ovarian eggs on September 1, 1958.

Hydrophiidae

The numerous species of sea snakes are all alike in being venomous, with elapid-like fangs and venom. However, they differ greatly in degree of specialization for marine life. They are largely restricted to the tropics and subtropics and most occur in the Indian Ocean, especially near its northern coasts and in the southwest Pacific in the Malaysian and Indonesian regions.

Sea snakes are known to congregate at certain times of year in connection with their breeding cycles. At the time of birth of their

young (or egg-laying in *Laticauda*) they may concentrate in large numbers on certain small rocky islets. Taylor (1965:981) stated: "I have seen very large numbers of the serpents identified as *L. colubrina* on the small island of Bubuan, Sulu Archipelago. Here I have observed large females, with large broods of young. . . ." *Laticauda* is oviparous. Herre and Rabor (1949:283) described great concentrations of *L. semifasciata* on the island of Gato north of the Philippine Island of Cebu in the Visayan Sea. In summer both the snakes themselves and their eggs could be found in abundance in grottos and caves of the coral limestone. St. Girons (1964:185-214) described the habits of a species of *Laticauda* in New Caledonia in the southern part of the Tropical Zone. Sexual maturity is attained late in the second year. Eggs are laid in summer (December to February). In winter approximately half the population is concentrated ashore in crowded colonies, and dispersal occurs in September. *Laticauda* and *Aipysurus* represent the subfamily Laticaudinae, the more primitive sea snakes, that retain ventral scutes and have limited power of locomotion on land. All the remaining genera comprise the Hydrophiinae, which are even more specialized for marine life. They are helpless on land and do not voluntarily leave the water. All are viviparous and the young are born in the water (Taylor, 1965:990).

Large breeding aggregations of sea snakes have been observed. Copulation takes place in the water. Lowe (1932:43) described a great concentration of *Astrotia stokesii* in the Straits of Malacca. The intertwined snakes formed a line running parallel to the course of the observer's ship. After four hours of travel near the line, which had all that time been visible, the ship approached nearer and the observers ". . . were amazed to find that it was composed of a solid mass of sea-snakes, twisted thickly together. . . . When I say millions I consider it no exaggeration; for the line was quite ten feet wide, and we followed its course for some sixty miles. . . ." Smith (1943:440) who cited the above observations, mentioned a similar, but probably more local concentration in the sea off Quantan on the east coast of Malaya. "The whole sea around his yacht, he said, seemed to be alive with sea snakes, twisting and coiling together. They remained at the surface of the water and did not dive down and disappear as they usually do."

Volsoe (1939:41) studied the sea snakes of the Persian Gulf and the Gulf of Oman, and found that April and May comprise the breeding season for various species including *Enhydrina schistosa,*

Hydrophis cyanocinctus, H. lapemoides, Microcephalophis gracilis and *Praescutata viperina.* He cited literature reports indicating that the breeding season was February and March for *Enhydrina schistosa* and *Hydrophis cyanocinctus* in the Ganges Delta, but that in the Gulf of Siam the majority of species give birth to their young in March and April. Hatching of the eggs of *Laticauda colubrina,* was reported to occur in June, July and August on the islands near Singapore. Volsoe cited the following numbers of young in broods of sea snakes: *Astrotia stokesii*—12, 14; *Enhydrina schistosa*—7, 11; *Hydrophis cantoris*—6; *H. caerulescens*—2 to 6; *H. cyanocinctus*—3, 8, 9, 16; *H. fasciatus*—2, 4, 4; *H. lapemoides*—2, 2, 3, 5; *H. mamillaris*—4; *H. obscurus*—5, 6, 9, 10; *H. spiralis*—5, 7, 14; *H. stricticollis*—9; *Kerilia jerdonii*—3; *Lapemis curtus*—1 (in 4), 2 (in 7), 4 (in 1); *Laticauda laticaudata*—7; *Microcephalophis gracilis*—1 (in 1), 2 (in 5), 3 (in 1), 6 (in 1); *Pelamis platurus*—2; *Praescutata viperina*—3. Volsoe commented that with increasing specialization for marine existence there is a trend toward smaller litters of young, correlated with relatively large size of the young at birth. Visser (1967:219) reported females of *Pelamis platurus* containing eggs or embryos, on the coast of South Africa in February-March, May 18, July 28, September 20 and October 13. Large embryos occurred in February-March, May, and October, indicating breeding through much of the year. Broods numbered 1, 2, 3, 4, 4, 4, 5, and 6 young, average 3.6. Visser commented that this average was higher than in some of the less specialized hydrophiines, contrary to Volsoe's statement. Minton (1966:148) reported a female of *Enhydrina schistosa* from near Korangi, West Pakistan, that contained four fully developed embryos on July 10.

Even within a few degrees of the equator, at Surabaya, Java, Bergman (1943:156) obtained evidence of a restricted breeding season. He examined nearly 800 sea snakes, *Thalassophis anomalus, Lapemis hardwickii, Enhydrina schistosa, Hydrophis fasciatus, H. brookei* and *H. cyanocinctus.* His data indicated a single ovulation cycle each year. Pregnant snakes began to appear in April samples, increased rapidly in numbers in May and June, and made up about 75 per cent of the adult females through July, August and September, but then declined in numbers through October and November. Wall (1921:387-423) mentioned reproductive state in a few individuals, most of which fall in line with the annual cycle described by Bergman in Java. Gravid females were noted as follows: one of *Kerilia imbricata* on June 25; one of *Astrotia stokesii* in August; one

(in an early stage) of *Enhydrina schistosa* in November and many in December, January and February; 12 of *Lapemis curtus* from June 20 to July 12; one of *Pelamis platurus* in late March. A 9½-inch juvenile of the latter species was recorded on May 11.

Two species have been studied north of the tropics in southern Japan. For one of these, *Laticauda semifasciata,* Fukada (1965:73) found that mating takes place in September and October and egg-laying occurs from mid-October to early December. Seven eggs were laid by each of two females. A clutch laid on September 29 hatched the following March 4, after 160 days' incubation at 28° C. Fukada reported that a female *Hydrophis melanocephalus* gave birth to young on October 16, 1928, one month after capture.

At Bahía Honda, Panamá, Myers (1945:22) noted nocturnal activity of the pelagic sea snake *(Pelamis platurus)* and collected a series on March 1. They were of two distinct sizes with no intermediates; all were either adults, or young 220 to 311 mm in length, the smallest still showing faint umbilical scars.

Viperidae

There are both oviparous and viviparous types in the family. Viviparity is the more common, and the northernmost vipers are viviparous, but there are both oviparous and viviparous species, in some numbers, both in the Temperate Zone and in the tropics. The true vipers are venomous, front-fanged, usually heavy-bodied snakes of Africa, Europe, and Asia. Although mainly tropical they are remarkable for ranging farther north than any other snakes.

Atheris

These are arboreal, viviparous vipers of tropical Africa. Loveridge (1942: 314) mentioned a specimen of the Great Lakes bush viper, *A. nitschei,* from Central Africa that contained nine embryos on January 18. Loveridge (1936: 280) noted that a female of the green bush viper, *A. squamigera,* from Sipi, East Africa, was distended with small embryos on December 18, 1933, but a series of 49 snakes from Kaimosi, February 10 to 28, 1934, contained none that was gravid.

Bitis

These large heavy-bodied African vipers are viviparous. There seem to be well-defined breeding seasons, at least in some of the regions inhabited.

Bitis arietans.—In South Africa, FitzSimons (1919:223) stated that he had often observed courtship in captive puff adders in October, November, and

December, that in confinement the snakes had often given birth in March, April, and May, and that in April 1910, five females all gave birth to young. He reported that one female contained 27 fully developed eggs on June 24 and another contained 24 eggs on July 1.

In southern Rhodesia, Broadley (1959:76) noted a pair of captive puff adders mating on August 26, 1956. He wrote that a 30-inch female gave birth to a brood of 35 young on December 2, 1957, and a 32-inch female contained 37 fetuses in early November. Loveridge (1953:295) wrote of this species in East Africa: "Data suggesting that young vipers are born in November were furnished by the finding in the garden at Chitala (mid-December) of three snakes so young their umbilical scales were not always healed. . . ." Larger young were found in mid-February. In the Rukwa Valley of southwestern Tanganyika, Robertson, Chapman and Chapman (1962:431) obtained a sample of 24 adult females in year-round collecting and obtained gravid specimens from May to August. Eggs or embryos in gravid females averaged 42 (23 to 56).

Bitis atropos.—FitzSimons (1962:345) stated that eight to 15 young are born, usually in March or April, in this South African species.

Bitis caudalis.—FitzSimons (1962:351) stated that the 12 to 19 young of the horned adder are born in summer—December to February.

Bitis cornuta.—For the South African many-horned adder, FitzSimons (1962:349) stated that the usual litter is 12 (8 to 20) born in February or March.

Bitis gabonica.—Loveridge (1942:311) reported a gravid female Gaboon viper containing 43 large eggs on July 1, at Magrotto in central Africa.

Bitis nasicornis.—In the Belgian Congo, Schmidt (1923:144) reported a female rhinoceros viper containing 31 young 200 to 210 mm long on February 16, 1920. Loveridge (1942:312) obtained three nongravid females in November and February.

Causus

The night adders are an African group of oviparous vipers that are mainly tropical in distribution. The observations of Woodward (1933) on a captive *C. rhombeatus* indicate an extremely high reproductive potential, with individual females having the capacity to produce successive clutches of eggs at intervals of a few weeks.

Causus defilipii.—In southern Rhodesia, Broadley (1959:75) reported that a female laid two eggs on January 1, 1956, and was seen to mate on the following day. Many hatchlings were noticed in February and March. FitzSimons (1962: 330) stated that the usual clutch is six to eight eggs, laid in summer, and that incubation takes 3½ months.

Causus lichtensteini.—Loveridge (1942:309) obtained gravid females of this night adder in central Africa (Mubango, Bisu, Budongo, Kibale Forest) on November 19 and 30 and December 4.

Causus resimus.—Loveridge (1942:308) found six eggs in a female green night adder collected January 27 in East Africa.

Causus rhombeatus.—Woodward (1933:189) made a remarkable series of observations on a checkered night adder kept in captivity at Accra Ghana from March 14, 1931, until January 18, 1932. This was a female two feet and two inches in length. She laid clutches of eggs on the following dates: April 26, May 22, June 16, July 13, August 18, September 18, and October 14, after which the snake was removed from her individual enclosure and placed with others and no more detailed observations were made. Between clutches the female had an active feeding period of several days during which she took numerous toads, and underwent sloughing. Eggs in the several clutches numbered 11, 14, 17, 18, 16, 15, and 15, respectively. The female was kept in isolation until the seventh clutch was laid, and attempt was made to incubate each clutch. Fertility was 100 per cent in the first and second clutches, 64.7 per cent in the third, and 55.5 per cent in the fourth; subsequent clutches were all infertile.

In East Africa, Loveridge (1936:292) obtained gravid females on August 2 and October 5. There were 14, 22, and 26 eggs in these clutches. In southern Rhodesia, Broadley (1959:73) observed that a female laid 14 eggs on October 8, 1957. FitzSimons (1962:328) stated that in the Temperate Zone of southern Africa only one clutch is produced annually, with 12 to 26 eggs, and that mating is usually in early spring.

Echis

The saw-scaled vipers include two desert-living, medium-small but highly venomous species of northern Africa and southern Asia. Seemingly they differ in breeding habits, *E. carinatus* being viviparous whereas *E. colorata* is oviparous.

Echis carinatus.—Smith (1943:490) stated that litters consist of three to 12 young and that in the vicinity of Bombay, India, births are in April, May and June. In West Pakistan, Minton (1966:160) recorded three to 11 embryos in females collected during late March and April. Young were collected from early June through the first half of August and a captive female gave birth to nine young on July 23.

Echis colorata.—This species was studied by Mendelssohn (1965) in Israel. He found that *E. colorata* is oviparous. Clutches average 7.6 eggs, but females do not produce every year. Under unfavorable conditions gravid females resorb the eggs. The eggs are relatively large and hatchlings retain a large reservoir of yolk to sustain them in their early development.

Pseudocerastes

These horned vipers occur in southwestern Asia in desert regions. According to Mendelssohn (1965) *P. fieldi* in Israel is oviparous, but the eggs are laid with development of the embryos well advanced. Clutches are larger than in *Echis carinata.*

Vipera

This is chiefly a Eurasian genus but with species in North and East Africa. One species extends north into subarctic regions, and at least two are tropical,

although most of the area occupied is in the Temperate Zone. Most species are viviparous but at least two are oviparous. In the tropics there seems to be some breeding activity throughout the year, but in the far North the breeding season is concentrated and individual females may produce young only once in three or four years.

Vipera ammodytes.—Fuhn and Vancea (1961:316) wrote that in Romania mating of the sand viper occurs in the last week of April or the first week in May. The young, four to 18 per litter, are born in late August or early September.

Vipera aspis.—St. Girons (1957) studied the cycles of the reproductive organs in the asp viper in west-central France at about 47 degrees north latitude. He found that in the male there is some spermatogenic activity throughout the year, but that this activity is most intense in May and in late August and early September. Courtship and copulation occur only in mid-May and in late September. Ovulation occurs between the tenth and twentieth of June and parturition occurs in early September. From four to 12 eggs are ovulated. In the female the cycle is normally biennial. In the spring following parturition, new follicles enlarge, but never attain a length of more than 20 mm and undergo atresia in early June. At the northern extreme of the range the female's cycle becomes triennial. According to St. Girons this is a matter of temperature deficit; in the relatively short and cool growing season the female cannot acquire and store sufficient energy to reconstitute herself and prepare for another pregnancy after just one season of rest.

Vipera berus.—Vainio (1931) and Volsoe (1944) studied the reproductive cycle of the common adder in northern Europe. In this northern part of the range the female may have a three-year breeding cycle requiring two growing seasons to regain her fecundity after a season of pregnancy. Usually ovulation occurs in late May and the young are born in the first two or three weeks of August. Litters vary, with from six to 20 young, but fully mature females usually produce 10 to 14. Some males attain sexual maturity at an age of 3½ years but females produce their first litters at an age of five years. In the British Isles and most of Europe there is an annual breeding cycle (Smith, 1951:252). In Romania, Fuhn and Vancea (1961:328) found that impregnation occurs in April or May and the young are born in August or September.

In the Swiss Alps, Saint-Girons and Kramer (1963:212) found that the season of activity is shortened by 1½ to two months, even as compared with Danish populations. As a result ovulation occurs only in biennial or triennial cycles, at the end of May, and gestation lasts until shortly before hibernation. Insemination may occur from April to June.

Vipera russellii.—In Ceylon, Wall (1921:511) found that there were gravid females of Russell's viper every month of the year, but young were most often born in the period May to November, and especially in June and July. For India the same author (1907:12) mentioned gravid females in March, April, May, July, and November, and births in June (5 instances), July (2 instances), and September (one instance). He listed 19 litters or complements of eggs or embryos in gravid females, as follows: 1, 9, 9, 14, 15, 18, 18, 21, 24, 25, 33, 36, 39, 40, 40, 40, 55, 62, 63 (average 29.6). In West Pakistan, Minton (1966:157) was informed that young are usually born in June, with 20 to 25 in an average litter.

Vipera ursini.—In Romania, Fuhn and Vancea (1961:328) found that impregnation occurs in April or May and young are born from July to September. Sexual maturity is attained in the third year.

Vipera xanthina.—In Israel, Mendelssohn (1963) found that copulation of these snakes occurs in May, and that the species is oviparous. Eggs numbering up to 22 per clutch, are laid in August, and their incubation requires from 39 to 62 days depending upon the temperature. Mendelssohn mentioned *Vipera lebetina* as another oviparous species within the genus.

Crotalidae

The pit vipers are sometimes allocated as a subfamily of the Viperidae. They are prevalent in both temperate and tropical regions of Asia, North America and South America, but are absent from Africa and Australia. The many New World species of *Bothrops, Crotalus,* and *Sistrurus* all are viviparous. The monotypic Neotropical *Lachesis* is the only genus that is entirely oviparous, but *Agkistrodon* and *Trimeresurus* each have both oviparous and viviparous species. The rattlesnakes are best represented in the Temperate Zone. Those that have been studied seem to have births concentrated in a period of weeks in late summer and autumn. The same statement applies to species of *Agkistrodon* and *Trimeresurus.* In *Crotalus* and *Agkistrodon* a biennial breeding cycle for females seems to be common.

Agkistrodon

This genus includes three North American species and several others in Asia, one extending west to southeastern Europe. The North American species are viviparous, but at least two of the Old World species are oviparous. One of these is Malayan, the other inhabits southern China. The viviparous species of the Old World occur far north in the Temperate Zone, and in high montane habitats, but also in the tropics. Of the oviparous species *A. rhodostoma,* at least, guards the eggs during their incubation. Reproduction is best known in the North American copperhead and cottonmouth. In these species there is usually a biennial breeding cycle in the female, but individuals deviate from this pattern. Mating occurs most frequently in spring, but also at other times of year. Female copperheads are gregarious in summer while they are pregnant, and there is a tendency for the female and her brood to remain together for at least a few days after parturition.

Agkistrodon acutus.—This is a large Oriental pit viper which in some respects resembles the North American copperhead. However, it is oviparous. Pope (1935:389) mentioned females that contained 20 and 26 eggs—indicating an unusually high reproductive potential for a crotalid. He also mentioned an embryo more than three inches long in a gravid female, hence much of the embryonic development perhaps is passed in the body of the mother before egg-laying occurs.

Agkistrodon bilineatus.—Alvarez del Toro (1960:189) wrote that in Chiapas, the cantil has a litter of about a dozen young.

Agkistrodon contortrix.—My eleven-year field study of the copperhead in northeastern Kansas (Fitch, 1960:272) led to the following conclusions regarding reproductive cycles of the species locally.

"Males become sexually mature in their second summer, usually many weeks before they have attained an age of two years. At sexual maturity they may be as small as 420 millimeters in snout-vent length. . . . Most females become sexually mature after their third hibernation and produce first litters when they are approximately 520 mm. Thereafter, females normally produce litters in alternate years. Copulation may take place in any month throughout the snakes' season of activity . . . most frequently in April soon after emergence from hibernation, and in the latter half of May, the season when ovulation occurs. Births are concentrated in the first half of September but may occur in late August or early October."

The conclusion that females produce litters in alternate years was tentative, based on the fact that many adult females captured in summer are not gravid, and ". . . of ten females originally recorded as gravid, three were not gravid when recaptured in odd-numbered years, and seven were again gravid when recaptured in even-numbered years; [evidence that this] pattern may not hold throughout the range of the species and particularly in the southern part is indicated by Allen's (1955:228) record of a female from Texas that produced successive litters on August 24, 1954 and August 20, 1955."

New evidence has not entirely borne out the suspected pattern of fecund seasons in alternate years in individual females. Anderson (1965:268) wrote that a captive female in Missouri bore successive litters on September 1, 1946 and September 25, 1947. Also, Anderson recaptured a gravid female (previously marked and released) on July 30, 1958, and recaptured it a second time on September 3, 1959, when it was again gravid and about to give birth to a litter. My own field work, continued through the seasons 1960 to 1966 after publication of my copperhead study, yielded additional records of significance in this connection. Four seemed to conform to the pattern of production in alternate years, as follows:

No. 1 nongravid on May 19, 1960 and again on August 2, 1962
No. 2 gravid on June 1, 1960 but nongravid on July 10, 1961
No. 3 nongravid on July 10, 1961 and again on June 25, 1963
No. 4 nongravid on June 20, 1962 and gravid on July 13, 1963

However, in five other instances there was nonconformity with this pattern as the following records show:

No. 5 nongravid on May 19, 1960 and gravid on June 12, 1962
No. 6 nongravid on July 17, 1960 but gravid on June 16, 1966
No. 7 nongravid on July 10, 1961 and again on July 1, 1962 (same individual as No. 2)
No. 8 gravid on July 5, 1961 and nongravid on July 31, 1965
No. 9 gravid on May 30, 1963 and nongravid on June 5, 1965

Seemingly, the female copperhead tends to have a biennial breeding cycle, but with frequent deviations. Individuals may produce litters in two successive years, or may go for two years without producing young. In six summers, 1960 through 1966, 142 captures of adult female copperheads were made, and these

involved different individuals except for a relatively few recaptures, as listed above. Most were obtained by funnel-traps set in grassland, and 81 of those captured were nongravid whereas only 42 were gravid. Summer collecting along hilltop ledges, however, has demonstrated that the population remaining in those situations consists essentially of gravid females. The ratio of gravid to nongravid among those trapped in grassland showed progressive decrease in successive months, perhaps indicating that in advanced pregnancy the females have an increasing tendency to return to the rock outcrops and remain relatively inactive.

	late May	June	July	August
No. of adult females in sample	24	41	36	22
Percentage of females gravid	46.0	41.4	27.8	18.3

In order to determine whether the reproductive cycle in the copperhead is notably altered by climatic factors such as those between the northern and southern extremes of the range, I examined a series of 95 from Terrell County, Texas (intergrades between *A. c. laticinctus* and *A. c. pictigaster*) in the University of Texas collection, all taken in late June and early July, 1949. In maximum and average size these copperheads were notably smaller than Kansas populations (which in turn are smaller than those from the northeastern United States). Whereas the smallest fecund females in Kansas are approximately 530 mm snout-vent, five out of the seven gravid females in the Terrell County series were below this size, and one was only 430 mm. Because Kansas females typically attain this length at an age of two years, and the growing season in Texas is longer, it seems that two-year-old females may be fecund in the southern part of the range. Ten other females in the range 430 to 490 mm were all nongravid, suggesting that the smallest gravid individual was unusually precocious. The more mature females 480 to 578 mm snout-vent, included six gravid and nine nongravid individuals, indicating that, in southwestern Texas, as in Kansas, a substantial proportion of the adult females are not fecund.

The seven gravid Terrell County females had an average of 3.0 eggs (two with two, three with three and two with four) indicating a relatively small average litter as contrasted with a mean of 5.02 for 115 Kansas litters and a mean of 6.16 for 55 litters of *A. c. mokeson* from the eastern United States.

Agkistrodon halys.—This is a widely distributed Asiatic pit viper with a relatively northern distribution. Pope (1935:395) presented data concerning reproduction in a series of females from China, Korea and Japan. Recorded birth dates were "September" (three instances), "October," October 3, 4, and 16. For 19 counts of eggs in females, or of young in litters, average was $8.05 \pm .62$, ranging from three to 12. Fukada (1962:16) studied the mamushi, *A. h. blomhoffii* in Japan. In 14 litters born in captivity the average was 5.0 (2 to 13). Of 69 young, 53.6 per cent were females. Birth dates ranged from August 31 to October 14 but were mostly in the period September 11 to 21.

Agkistrodon hypnale.—Smith (1943:500) stated that the hump-nosed viper is viviparous, producing from four to 10 young.

Agkistrodon nepa.—Wall (1921:556) recorded a female of the Ceylon hump-nosed viper containing eggs "in an early stage of development" on May 16. The species is viviparous.

Agkistrodon piscivorus.—Wharton (1966) studied a population of the cottonmouth at Cedar Keys, Levy County, Florida, and found that ovulation occurs in late May and early June (seemingly somewhat later than on the adjacent mainland). Evidence of a biennial reproductive cycle was derived from the fact that in 24 female reproductive tracts collected from May 1 to 20, 11 had ripening eggs and 13 did not, and among 34 females taken from June 1 to September 15, 16 were gravid and 18 lacked embryos. Thus about half of the adult females neither ovulate nor bear young in any given year. Wharton determined the average litter to be 5.5 young—fewer than on the mainland but averaging somewhat larger. (Allen and Swindell, 1948:11, found an average of 6.6 embryos in broods ranging from 12 to 3, in 31 gravid females from the Everglades.) Wharton found that males are able to breed in the late summer or fall of their second year, at an age of 22 or 24 months, and females become fertile in the fall of their third year. Evidence from pair associations, and sperm found in females, indicated that at Cedar Keys mating might occur in spring, fall, or even winter.

Wharton emphasized the severity of the general environment and the seasonal nature of the snakes' food supply (gleaned from a heron rookery) at Cedar Keys, the site of his population study. Because of these circumstances it seemed possible that the biennial breeding cycle was a local pattern rather than a trait of the species as a whole. However, Burkett (1966:453) examined a substantial number of adult females from the range of the western subspecies *A. p. leucostoma* and obtained additional evidence of a biennial cycle. The smallest gravid female examined by Burkett had a snout-vent length of 455 mm, and of 69 females 450 mm or more in length, 29 were gravid. In the size range 450 to 499 mm only three of 14 were gravid and doubtless most were still immature. Eliminating this group, and considering only those over 500 mm in length, 26 were gravid in a sample of 55; 15 of 34 in the 500-599 range, and 11 of 21 in the 600-899 range were gravid. The ratios fit well with the trend to be expected if a biennial breeding cycle prevailed. A bit of contrary evidence cited by Burkett was the record of a Florida female which in captivity gave birth to litters of 14 and 12 young in two successive years. However, this snake while in captivity did not hibernate and hence its normal cycle may have been altered. In 27 gravid females Burkett found an average of 5.08 (1 to 14) eggs or embryos.

Agkistrodon rhodostoma.—Smith (1943:499) wrote that in Bangkok, Thailand, two females of the Malayan pit viper laid 13 and 30 eggs on August 1 and September 1. The females remained with their eggs and guarded them; hatching occurred in 42 and 47 days.

Bothrops

This genus includes many species of Neotropical pit vipers. All are viviparous. Some are tremendously prolific; the large fer-de-lance, for example, often has several dozen young at one birth, whereas the smaller species have

relatively few young. The fer-de-lance is known to give birth at various times of year.

Bothrops atrox.—I examined large series of fer-de-lances in the Bassler collection of the American Museum of Natural History. Unfortunately most of them had no specific dates, and the larger individuals usually were not intact but often consisted of only head and/or skin so that it was not possible to determine their reproductive status. Measurements had been recorded in the field by the collector. A series of 191 were accompanied by specific dates and among these the seasonal distribution of young is significant. Unknown variables are the growth rate of the young and their size range at birth.

No definite conclusions can be drawn from these figures, but it seems that young of the smallest size group are rather evenly distributed throughout the year, suggesting a year-round breeding season in this part of the range, near the equator. The smallest young were three collected in March which were, respectively 166, 165 and 152 mm snout-vent. Probably the usual size at birth is considerably larger.

In British Guiana, Beebe (1946:50) recorded gravid females on May 9 (16 eggs), June 19 (9 eggs), September 25 (8 fetuses nearly full term) and

Table 9. Monthly Size-distribution in 191 *Bothrops atrox* from Iquitos, Peru.

Snout-vent length (mm)	Numbers in monthly samples											
	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Adults 1000 mm or more	2	1	3	1	3	..	1	2	2	6	..	5
Subadults and large yg. 600-999 mm	3	5	14	2	2	2	..	5	3	5	4	8
Young 300-599 mm	5	6	7	6	2	5	3	4	5	22	8	11
Small young less than 300 mm	4	1	3	1	2	..	..	4	..	6	4	3

October 20 (11 large embryos). Hirth (1964:453) made observations on the fer-de-lance on the Caribbean coast of Costa Rica and found 48 to 86 embryos in gravid females examined from June to September. He cited published records of birth on September 25 (Honduras) and November (Trinidad), and litters of 28, 38, 57, 64, 65, 71 and 71 young. In Panamá, Sexton and Heatwole (1965:42) recorded a female containing 32 eggs on December 23, 1961. Mole (1924:266) stated that on Trinidad the young are born from September to January inclusive, and he mentioned litters of 29, 30, 32, 56, and 56.

Bothrops insularis.—Amaral (1921:87) wrote of this insular species found only on Queimado Grande Island, São Paulo, Brasil, that the breeding season begins in August and lasts until the middle of September.

Bothrops nummifer.—Rokosky (1941:267) recorded the birth of two litters of tommygoffs. A shipment of the snakes was received at Chicago on March 16, 1940. On July 17 a 22-inch female gave birth to 21 young, and on July 25

a 28-inch female had 17 young, then died and was found to have six more young still in her oviducts. In British Honduras, Neill (1962:243) obtained juveniles 246 and 278 mm in length on August 28 and September 5. The umbilical scar was prominent in the smaller individual, partly healed in the larger. Neill speculated that both probably had been born in August.

Crotalus

This large genus includes the typical rattlesnakes, a group occurring from Canada southward through tropical South America, but having its greatest diversity in arid parts of northern México and the southwestern United States. A tremendous amount of information on their reproduction has been assembled by Klauber (1956 and earlier papers) along with other aspects of their natural history and systematics. The rattlesnakes are all viviparous. They tend to be gregarious hibernators, and mating may occur at the time of spring emergence and/or when aggregations form in late autumn. The adult females while they are gravid in summer, may also be somewhat gregarious. Study of populations of several species has demonstrated or at least suggested a biennial breeding cycle in the females, but this trend may not apply in relatively mild climates with long growing seasons. Number of young per litter varies widely. In general the large species have more numerous young in their litters, whereas small species have relatively few young per litter and these are relatively large at the time of birth.

Crotalus atrox.—No detailed study of the ecology and reproductive cycle of the western diamondback has as yet been made, but numerous miscellaneous notes concerning observations in the field and on captives are available. Klauber (1956:691) recorded copulation dates in the field on March 25, April 13, and August 19; and in captivity in December (date not specified), on December 29, in May (date not specified), and on August 5. Lowe (1942:261) recounted an incident occurring in Kern County, California on September 20, 1941—the tracks in the sand of two adults were found to meet and continue on together into a burrow, and the snakes when dug out were found to be male and female. Possibly mating had occurred. Lowe mentioned a similar incident that occurred in Riverside County, California, on October 18, 1941, and he also mentioned a mating on October 11, 1941, of a pair of captives from Indio, California.

Tinkle (1962:306) studied a local population in northwestern Texas, the northern part of the species' range. The collections were made at dens in winter. Two types of adult females were noted, those with large yolk-filled follicles and those in which follicles were relatively minute. The latter group mostly showed ovulation scars (corpora lutea) indicating ovulation in the preceding spring. The author concluded that females of the population studied had a biennial breeding cycle. However, of 106 adult females 70 had enlarged follicles (and mostly lacked corpora lutea) whereas only 36 were "nonreproductive" (with small follicles and mostly having corpora lutea)—a notable deviation from the 1-1 ratio that might be expected if a biennial cycle prevailed. Tinkle suggested the possibility that his sample was biased somehow by the method of collection, and thereby caused to deviate from the expected 1-1 ratio. It seems equally plausible that the unbalanced ratio indicates that about two-thirds of the adult females actually are reproductive each year, and only

about one-third fail to ovulate. Perhaps nutrition is the determining factor. Tinkle found that in snakes of similar weight, the quantity of stored fat was generally greater in the reproductive females, but there was considerable overlapping. He found that females mature at an age of three years and snout-vent length of 900 mm. Reproductive females contained from six to 19 ripe eggs, and the number was correlated with the size of the female. Tinkle emphasized the desirability of obtaining similar data from the southern part of the species' range to compare with his data from northwestern Texas. Klauber (1956) obtained figures for 36 litters from his examinations of gravid females and from the literature. Litters averaged 10.16.

Crotalus basiliscus.—Little information is available concerning this Mexican species. Perkins (1943:109) mentioned a litter born in captivity at the San Diego Zoo on June 27, 1938. On August 17, 1940, two survivors of this litter were observed copulating—at an age of two years, one month and 20 days. The same pair was again observed in copulation on August 31, 1941. Marcy (1945:169) mentioned a large female received on May 3, 1944, which on July 7, 1944, gave birth to 29 offspring, and also discharged four atrophied eggs. The few dates available suggest a breeding schedule much different from that of more northern rattlesnakes, with copulation occurring in late summer and birth in early summer. Klauber (1956:702) recorded counts for 13 litters which contained from 14 to 60 young with an average of 33.1, indicating that this rattlesnake is far more prolific than any of the more northern species.

Crotalus cerastes.—Klauber (1956:683) recorded copulation in a pair of captive sidewinders on May 11, 1944, two days after their capture, and another captive pair mated on October 11. In the field, copulation has been recorded on April 21, May 1, and May 7. Stebbins (1954:473) mentioned litters on August 9 (Huachuca Mts., Arizona) and July 21 (Terrell County, Texas). Klauber (1956:701) found litters of 5 to 18 in gravid females examined. For the 37 litter counts recorded by him, I obtained an average of 9.44.

Crotalus durissus.—Alvarez del Toro (1960:196) gave size of broods in Chiapas as 20 to 41.

Crotalus horridus.—The widely distributed, eastern, timber rattlesnake is one of the best known rattlesnakes, but there has been no thorough study of its reproductive cycle. It is one of the more northern rattlesnakes, and hibernates in communal dens, sometimes in large aggregations, often with copperheads, rat snakes, and other species. Seemingly mating usually occurs soon after emergence, with ovulation a few weeks later, and the young born in late summer or autumn. Some dates of birth are: August 26, 1936, in Minnesota (Edgren, 1948:132); September 8, 1933, in New Jersey (Trapido, 1939:230); September 12, 1951, in Ohio (Triplehorn, 1955:249); late August in Illinois (Smith, 1961:273); and September 1 in Missouri (Anderson, 1965:294). On the University of Kansas Natural History Reservation in northeastern Kansas I have found young having only a "prebutton" (hence, probably only a few days old) on September 30, 1950, and October 1, 1951. Litters of young have been recorded as follows: 10 (Trapido, 1939:230); 7 (Edgren, 1948:132); 7, 10, and 11 in Louisiana (Clark, 1949:260); 12 (Triplehorn, 1955:249); 8 and 9 (Smith, 1961:273); 5, 8, 8, and 19 (Anderson, 1965:289, 294). In

northeastern Kansas I have recorded 5, 6, 11, and 11 large eggs in females palped or dissected. It has not been learned whether there is an annual or biennial cycle in the timber rattlesnake. Klauber (1956:701) recorded counts of 5 to 17 young in 51 females and his counts yield an average of 10.01.

Crotalus lepidus.—Kauffeld (1943:607) reported the birth of a litter of four rock rattlesnakes on August 9, 1941, in southern Arizona. Minton (1959: 52) mentioned a female that gave birth to three young on August 23, and on August 4 he found a juvenile that appeared to be only a few days old in western Texas. Stebbins (1954:473) reported births on August 9 (female from Huachuca Mountains, Arizona), and on July 21 (female from Terrell County, Texas). He wrote that six females contained two to eight, average four, young. Klauber (1956) reported 14 litters with an average of 3.85 young.

Crotalus pricei.—Kauffeld (1943:353) reported that a female from southern Arizona gave birth to six young on August 19, and Stebbins (1954:477) reported births of five young on July 28 and six young on August 18. Klauber (1956) examined 11 gravid females that had from three to eight embryos, average 5.84.

Crotalus ruber.—Perkins (1943:109) noted copulation on February 18, 1937, in a pair captured a few weeks before. On August 10 the female gave birth to three young and aborted three eggs. On March 26, 1941, another female and a male, both captives for several years, mated and produced young on August 14. The same pair mated again on March 29, 1942, and the litter that resulted was born 152 days later. The same pair was observed to mate a third time on March 21, 1943. Klauber (1956:685) observed a copulating pair in San Diego County, California, in early April. In 49 gravid females examined by Klauber, numbers of young ranged from three to 20, and averaged 8.43.

Crotalus scutulatus.—Werler (1951:47) wrote that a female from Terrell County, Texas, had three young on July 21, 1950. Woodin (1953:294) related that on July 22 two adult females were dug out and three apparently newborn young were found with them. McCoy (1961:140) observed many recently born young on the highway near Robles Junction, Pima County, Arizona, on August 11, 1958. Klauber (1956:701) examined 14 females and found two to 11 young, average 8.10.

Crotalus viridis.—This species is widespread in the western half of the United States.

Several local studies have been made in different parts of the geographic range. Rahn (1942:233) and Ludwig and Rahn (1943:15) studying the prairie rattlesnake in the northern part of its range, noted that the adult females at the hibernation dens formed two distinct groups. There were "ripe" females destined to ovulate in late spring, in which ovarian follicles were already much enlarged, and post-parturient females in which ovarian follicles remained small. It was concluded that in the female prairie rattler there is a two-year breeding cycle. In the first year eggs in the ovaries remain small, but they grow rapidly in the summer of the second year and are large when the snakes are ready to enter hibernation. Copulation may occur in the autumn or in early spring, and upon ovulation in late spring the eggs are fertilized by stored sperm in the oviducts. In a large series of prairie rattlesnakes from near Plattesville, South

Dakota, Klauber (1956:687) found 59 adult females, of which 30 were in the "ripe" stage and 29 were post-partum. In Tooele County, Utah, Glissmeyer (1951:27) studied the population of Great Basin rattlesnakes returning to a hibernation den over an 11-year period, and found that from 63 per cent to 12.5 per cent of the adult females captured in different years were productive. Some of the annual samples were small, but for the entire 11-year period the ratio of productive to nonproductive females approximated 1-1, leading the author to conclude that a biennial breeding cycle prevails. However, he might equally well have concluded that the ratio of reproductive females varies greatly from year to year in response to weather, food and other environmental factors.

At the San Joaquin Experimental Range in the Sierra Nevada foothills of central California, I studied a population of *C. v. helleri* from 1938 to 1946 (Fitch, 1949:538). Of 33 adult females dissected in 1940 and 1946, 16 had enlarging ova and 17 lacked them. Hence it was concluded that an individual female may breed only in alternate years. However in March, April, and early May, the eggs in all females were still relatively small (in contrast to the findings of Rahn, 1942; Glissmeyer, 1951; and Klauber, 1956, in more northern regions) and ovarian follicles did not attain full size until nearly mid-June. Consequently reproductive and nonreproductive females were not readily distinguished early in the season. Further studies are needed before definite conclusions can be drawn regarding the species' reproductive cycle on the West Coast. Klauber (1956:701) accumulated many records of litters from his own examinations of gravid females and from published literature, showing marked differences in productivity between the subspecies as follows:

307 *viridis* (Great Plains) averaged	11.40 ± .19
49 *oreganus* (northwest Coast) averaged	10.61 ± .98
12 *helleri* (California) averaged	7.91 ± 1.15
38 *lutosus* (Great Basin) averaged	7.85 ± .48
10 *nuntius* (northern Arizona) averaged	7.00 ± .78
7 *caliginis* (Los Coronados Islands) averaged	2.57 ± .34

Lachesis

This genus includes only the giant Neotropical bushmaster, *L. muta*, the only oviparous crotalid in the New World; the species is scarce, hence there are few records of its reproduction. Mole (1924:268) in Trinidad first observed and reported the oviparous habits, after a female kept by him laid a clutch of 10 or 12 eggs in July, 1903. Mole quoted a field observer, Reginald Carr, who claimed to have found natural nests in burrows of mammals on many occasions. "There were never more than ten or twelve [eggs in a clutch]. He had known six and had seen two and three and once only one."

Amaral (1926) wrote that one captured in Maharu, Bahia, Brasil, laid 11 eggs on December 6, 1921, and that another which died on March 1 contained two oviducal eggs. Beebe (1946:48) wrote: "One female taken at Kartabo [British Guiana] on April 6 contained seven nearly formed eggs each three inches in length, and another snake captured on May 19 at Caripito had a 2½ inch shell-less yolk." The widely scattered dates suggest that there is no well-defined breeding season.

Sistrurus

Pygmy rattlesnakes and massasaugas are thought to be more primitive than the typical rattlesnakes of the genus *Crotalus*, but are viviparous like them. Recorded dates of copulation for the massasauga are in autumn but probably mating occurs in spring also.

Sistrurus catenatus.—Birth dates for massasaugas are August 19 and 30 in Illinois (Tobiasz, 1941:269) and August 11 in Ohio (Triplehorn, 1955:249). Klauber (1956:692) mentioned records of copulation at the San Diego Zoo on August 31, September 24, and November 9. For 54 litters, based on his own examinations of gravid females, and on published literature, he found from two to 19 young. I obtain an average of 8.16 ± .44 for his counts.

Sistrurus miliarius.—Klauber (1956:701) listed counts for 15 litters of young in the pygmy rattlesnake; numbers ranged from two to 18 and averaged 7.33 ± 1.05. Later, Carpenter (1960c:142) recorded an unusually large litter of 32 young born on August 6, 1959, at Lake Texoma, Oklahoma.

Trimeresurus

This is a genus of Oriental pit vipers, with several species, some tropical, others extending into the Temperate Zone or into high montane habitats. There are both oviparous and viviparous species, with various transitional stages. In the Japanese and Chinese species, mating is in spring and young appear in autumn, but nearer the equator in Ceylon seemingly there is no such well-defined breeding season.

Trimeresurus flavoviridis.—This is a large oviparous pit viper of the Loo Choo Islands. Fukada (1965:71) summarized much information published by Mishima in 1961, as follows: The mating season is from late March to late May and egg-laying occurs from early June to early August. Clutches of eggs ranged from three to 17 with an average of 8.7. The number of eggs was closely correlated with the size of the female, as follows.

Females of 110 to 119 cm averaged 4.4 eggs (3 to 7)
Females of 120 to 129 cm averaged 4.9 eggs (3 to 7)
Females of 130 to 139 cm averaged 8.0 eggs (3 to 11)
Females of 140 to 149 cm averaged 10.0 eggs (6 to 15)
Females of 150 to 159 cm averaged 12.4 eggs (10 to 17)
Females of 160 to 169 cm averaged 11.4 eggs (10 to 13)

The incubation period was 40 to 41 days. In the subspecies *T. f. tokarensis* of the Tokara Islands adult size is markedly smaller and observed clutches had fewer eggs (2, 4, 4, 5, 5). Hatching occurred from late August to early October.

Trimeresurus jerdonii.—This montane pit-viper of southwestern China is viviparous. Pope (1935:411-412) recorded birth of a litter on September 12, and recorded gravid females collected in May (2), June (1), July 3 to 12 (3), and August (1). In the broods found in gravid females or born in captivity, there were 2, 4, 5, 5, 6, 7, 7, and 8 young.

Trimeresurus monticola.—This is another montane Oriental pit viper, but, unlike the preceding species, oviparous. However, eggs are seemingly retained

inside the female until embryos are well developed. Nests are in plant debris and the female guards her eggs. Pope (1935:414) described nests found in Kuatun, China, in August. Eggs from three nests had hatched by September 12.

Trimeresurus okinavensis.—Fukada (1964:7) described reproduction in the mamushi. A female obtained in June, 1963, fed normally. She laid six thin-shelled eggs on August 28. After two days the eggs had gained 19 per cent in weight by absorbing moisture from the damp substrate. Three of the eggs hatched, one on August 31, a second sometime the following night, and the third after one more day. Incubation periods were thus only three to four days. Earlier observers have noted similarly short incubation periods. Fukada cited published records of egg-laying on September 10, and, in another instance, on September 12. Having a remarkably short incubation period, this oviparous pit viper is on the verge of viviparity. In a later publication, Fukada (1965:72) suggested that confinement of the female may have influenced somewhat the sequence of laying and hatching, and he cited another author (Takara) who observed a female in Okinawa (where the species is endemic) that gave birth to five young, some enclosed in membranes from which they soon escaped and others already free.

Trimeresurus stejnegeri.—Stejneger's pit viper is an Oriental arboreal species seemingly viviparous as large embryos have been found in females in summer. Pope (1935:422) recorded broods of 4, 3, and 3 embryos. Maslin (1950:463) recorded females containing seven and four oviducal eggs, the latter on March 31.

Trimeresurus trigonocephalus.—Wall (1921:562) reported gravid females of this arboreal Ceylonese species on January 12 and July 1. They contained five and 26 embryos. A year-round breeding season is suggested by these two records, falling at opposite times of year.

DISCUSSION AND CONCLUSIONS

Factors Affecting Reproductive Cycles

Snakes and lizards have evolved into many ecological types occurring from the deserts, rain forests, and high montane habitats of equatorial regions over most of the land area of the tropics, through the Temperate zones, and north even beyond the Arctic Circle. They have undergone notable adaptations to withstand heat and cold, drought and flood. Terrestrial, arboreal, fossorial, aquatic, and even marine types have evolved. There has been specialization for diets of foliage or other plant parts, of insects or other invertebrates, and of vertebrates of each class, over a wide size range.

In making such evolutionary adjustments the squamates have attained a great physical diversity of structures, proportions, sizes and colors. Accompanying these differences are altered reproductive habits, which involve the size, shape, and number of eggs, the

frequency with which clutches are produced, the rate of their development, the stage to which they develop before laying, and their tolerances to factors of the physical environment. Hence, great diversity characterizes the reproduction of the group as a whole.

Numerous interrelated factors affect reproductive cycles. These cycles may be determined by innate rhythms of the animals themselves as appears to be the case in certain cobras, and in the copperhead *(Agkistrodon contortrix)*, and other animals confined in zoos, far from their place of origin, which nevertheless reproduced regularly each year at the same time that they would have if they had remained under natural conditions. In others like the five-lined skink *(Eumeces fasciatus)* the breeding cycle seems to be triggered by a hibernation period, and upon emergence the animal undergoes rapid physiological change to prepare it for the season of reproduction. In still other kinds, like anoles *(Anolis carolinensis)* photoperiodicity controls the waxing and waning of the breeding season, but this phenomenon is much less general in reptiles (many of which spend their daily and seasonal inactivity periods in hiding places where they are shielded from the light) than in birds and mammals. In many kinds of tropical reptiles, the breeding cycle is influenced by the distribution of precipitation. In captivity several kinds of snakes have been found to vary in frequency of egg-laying and size of clutch, seemingly in response to amount of food consumed, and various lizards have been shown to be relatively unproductive in drought summers.

Some variable aspects of breeding cycles in reptiles are: length of time required for development from birth or hatching to maturity, number of young born in a litter or eggs laid in a clutch, normal length of interval between successive clutches or litters, the size of the adult animals, and the relative size of their newborn young or hatchlings.

In general, the fewer young there are in a brood or litter the larger they will be at birth or hatching. In some species the newborn young are slightly more than half the usual length of the adult female, whereas in other kinds the newly emerged young are less than one-fourth the length of the mother and of correspondingly small bulk. In general the smallest kinds of snakes and lizards have few young or eggs whereas the larger kinds are more prolific. Size difference between hatchling and adult is thus closely linked on the one hand with number of young and their survival

expectancy, but on the other hand is linked with behavioral aspects of species' ecology, and especially with food habits. The type of available food may impose sharp limitations on the minimum size of the young so that a stunted individual setting out in life at a size less than that which is usual for the species may have little prospect of survival. This applies especially to reptiles that are predators upon higher vertebrates. In other kinds, which are such generalized predators that they take a great variety of prey species, or undergo a change of habits during the course of their growth, and in which the young take kinds of prey different from those utilized by the adults, or whose prey species—*e.g.*, some fishes—themselves have an even wider size range between young and adult, the young reptiles are freed from such rigid restrictions to minimum size; presumably it is advantageous to the species to have its population dispersed over a wide size range thus reducing competition between individuals. The fer-de-lance, common garter snake, and common water snake are examples of such species in which the newborn young are relatively small and numerous.

Length of time required from birth or hatching to sexual maturity is an important aspect of each species' population dynamics linked with such factors as length of growing season, level of metabolism, and differential in size between adults and young. While those kinds which attain greatest body size and those kinds in which the young are smallest relative to adult size might be expected to require the longest periods of growth, the correlation is not close, and the time required for development is extremely variable. From rapid development in the tropics, where there is year-round activity, there is a noticeable trend to long-delayed maturity in seasonal climates where the growing season may occupy as little as one third of the annual cycle or even less. In small lizards of the warmer parts of the Temperate zones, and in both lizards and snakes in the tropics, sexual maturity may be attained in the first year of life. However, many kinds, including some in the tropics, do not attain sexual maturity until late in the second year. In the Temperate Zone even small lizards of some kinds *(Anguis, Ophisaurus)* may require as much as four or five years to reach maturity; but for the majority of species such information still is not available, and most that have been studied require a shorter period to mature.

Size of Brood

On the basis of a sample of 150 species of lizards and 100 species of snakes in which usual size of clutch or litter is fairly well known (Figs. 9 and 10) it can be stated that snakes are by far the more prolific of the two groups. For the snakes, seven is the most frequent number of eggs or young per brood, and most broods fall in the range two to 16, whereas in lizards the most frequent number is only two; most species have means falling within the range two to six but with some in the range seven to 15 and a few species with larger complements.

There are relatively few species—essentially those with broods of only one or two—in which the number of offspring is constant. For many kinds, the expected range is great. Newly matured females and those that are undernourished are the least productive; maximum complements can be expected only from those that are several or many years old, are near the maximum size for their species, and are well nourished.

Little is known about the size of complement in the more productive species. Several species of snakes have been known to produce complements of 100 eggs or more, and a larger number are known to have produced complements between 80 and 100. However, these species usually produce much smaller complements, and it is doubtful whether there are any that consistently average more than 50 eggs or young. For most such prolific species, only a few records are available and these cover a wide range, so that the normal quota for the species can only be guessed. The most productive genera known include the giant boas and pythons *(Eunectes, Python)*, some of the larger water snakes of America *(Natrix)* and Asia *(Xenochrophis)*, the Australian elapid tiger snake *(Notechis)*, the mud snake *(Farancia)* of the southeastern United States and mole snake *(Pseudaspis)* of South Africa among colubrines, two Neotropical crotalids *(Bothrops atrox, Crotalus basiliscus)* and a Paleotropical viper *(Vipera russellii)*. For lizards the largest clutches of 30 to 60 eggs are attained only by a few relatively large kinds—the large iguanas *(Iguana, Ctenosaura)*, the South American tegu *(Tupinambis)*, certain monitors *(Varanus)*, and some of the large chameleons *(C. dilepis, C. melleri, C. senegalensis)*. All these most prolific kinds of lizards are oviparous. One of the more prolific viviparous lizards is the horned lizard, *Phrynosoma douglassii*, which averages about 15 young and is known to produce as many as 31.

At the other extreme are the relatively numerous species of both snakes and lizards that produce small clutches or broods, with only one to four eggs or young. In the sphaerodactyline geckos there is only one egg per clutch, but eggs are seemingly produced in fairly rapid succession; reduction of the clutch to minimum size minimizes the handicapping of the gravid female, the eggs are well dispersed in time and space, and the hatchling is larger than it would be if the egg were crowded by others in the female's body. The most efficient production of single-egg clutches has been attained in anoles, in which the two ovaries alternate in their ovulations, so that at any one time the female usually contains two large or fast-growing eggs at different stages of development. Other lizards in which production of a single offspring at a time may be the general rule are the amphisbaenid, *Chirindia ewerbecki*, the teiid, *Bachia flavescens*, and of viviparous species, the South African *Platysaurus capensis* and the serpentiform fossorial skinks, *Typhlosaurus lineatus* and *Ophioscincus roulei*.

For most of the species of snakes and lizards herein included, the data were composites from various parts of the geographic range. Probably all species of snakes and lizards that are wide-ranging have both genetically and environmentally determined geographic variation in such traits as numbers of eggs or young produced, and timing of the breeding season, but for most the data are inadequate to show such variation. There are many species in Africa and Asia and a few in the Americas that range from equatorial regions into cool-temperate climates, and these provide particularly promising material for investigations of geographic variation in reproductive cycles, but as yet hardly any of them have been well studied. One example is the gecko, *Hemidactylus frenatus*, which breeds throughout the year in Java, but which has a relatively short breeding season, with hatching limited to July and August, in Japan.

In most of the widely distributed species of the United States latitudinal changes in the extent of the breeding season are demonstrable, but they are often less well marked than might be expected. In the northern states, the spring (or autumn) breeding season is relatively short and well defined, but southward it becomes longer and more diffuse. The brown-shouldered lizard *(Uta stansburiana)* is a good example. In the northern part of its range, where the winter is long and intensely cold, gravid females are to be found only in May, June and July, but in southern California

they have been found from March to December, and in Baja California have been found even in January and February. Thus in the north, a local population consists of several discrete annual age groups, whereas in the south there are individuals of intermediate ages. There is increasing clutch size from north to south in this species, with an average clutch of 2.7 in the northern part of the range, 3.4 in southern California, 3.8 in western Texas, and 4.2 at Phoenix, Arizona.

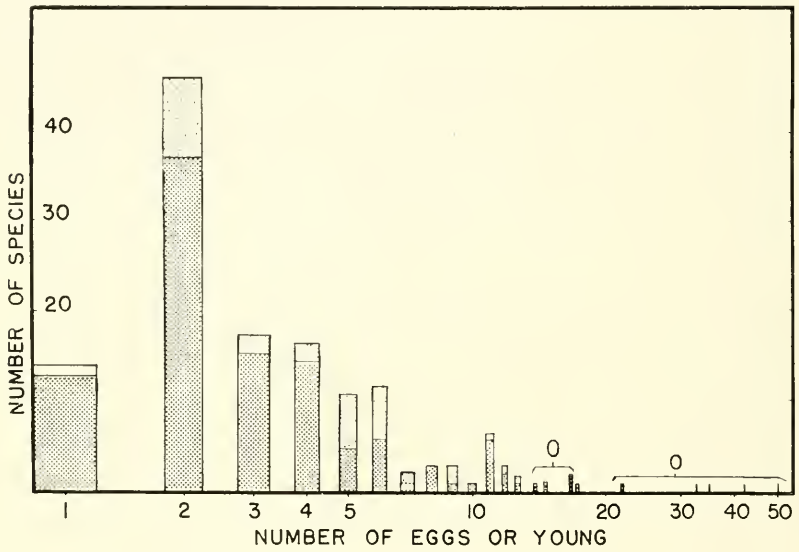


Fig. 9. Histogram showing typical size of brood (number of eggs per clutch or young per litter) in 150 species of lizards, as follows: BROOD OF ONE—*Gehyra variegata, Gonatodes albogularis, G. concinnatus, Anolis carolinensis, A. fuscoauritus, A. humilis, A. lemurinus, A. leptoscelis, A. limifrons, A. lionotus, A. tropidolepis, Cordylus cordylus,* and *Trogonophis ewerbecki;* BROOD OF TWO—*Acluroscalabotes felinus, Cnemaspis africanus, Coleonyx variegatus, Cyrtodactylus malayanus, C. pubisulcus, Gecko gecko, G. japonicus, Gymnodactylus geckoides, Lygodactylus capensis, Pachydactylus geitje, P. punctatus, Peropus mutilatus, Rhotropella ocellata, Rhotropus boultoni, Hemidactylus albofasciatus, Oedura ocellata, Amblyrhynchus cristatus, Sceloporus cozumelae, Uma inornata, U. notata, Calotes cristatellus, Draco melanopogon, Emoia callisticta, E. cyanogaster, E. cyanura, E. mivarti, E. pallidiceps, Carlia rhomboidalis, Leiolopisma aeneum, Leptosiaphos meleagris, Lipinia noctua, Mochlus modestus, Nessia burtoni, Scelotes bipes, Scincella cherriei, Trachydosaurus rugosus, Tropidurus albemarlensis, Ameiva festiva, A. quadrilineata, Neusticurus ecpleopus, Leposoma percarinatum, L. southi, Cnemidophorus hyperythrus, C. tigris, Xantusia henshawi, X. vigilis,* and *Anniella pulchra;* BROOD OF THREE—*Crotaphytus silus, Sceloporus chrysostictus, S. variabilis, Draco obscurus, D. quinquefasciatus, Goniocephalus grandis, G. liogaster, Mabuya rudis, Melanoseps ater, Scincella laterale, Sphenomorphus temminckii, Cnemidophorus deppii, C. exsanguis, C. guttatus, C. sexlineatus, Kentropyx calcaratus, Acanthodactylus pardalis;* BROOD OF FOUR—*Basiliscus vittatus, Callisaurus ventralis, Sceloporus graciosus, Uta mearnsi, Uta stansburiana, Urosaurus graciosus, Lep-*

A number of other species parallel the brown-shouldered lizard and each other in having increasing clutch-size from north to south, as follows: *Holbrookia maculata,* 4.9 in Kansas and 7.0 in New Mexico; *Sceloporus graciosus,* 3.6 in Oregon, Washington and neighboring areas, 4.2 in southern California and Baja California; *Gerrhonotus coeruleus,* 5.0 in Oregon and Washington, 6.3 in California; *Gerrhonotus multicarinatus,* 9.0 in Oregon, 11.7 in southern California; *Diadophis punctatus,* 3.5 in Michigan, 4.2 in Kansas, 5.2 in Florida; *Storeria occipitomaculata,* 7.2 in Michigan, 9.4 in a mixed sample from over the range as a whole; *Opheodrys vernalis,* 6.7 in northern Michigan, 8.8 in the Chicago region. However, in certain other species the reverse trend seems to apply; *Cnemidophorus tigris* has an average clutch of 3.4 in Colorado, but only 2.2 in western Texas, and *Scincella laterale* averages 3.8 eggs in Kansas and Missouri but only 3.1 in Texas and Louisiana. In various other species the trends in variation do not follow either of these patterns. For example, *Crotalus viridis* of the northern Great Plains produces an average litter of 11.4 but on Los Coronados Islands, off the northwestern tip of México, the litter averages only 2.6, and intermediate populations of interior California, the Great Basin and the southern Rocky Mountains average between 7 and 8. *Agkistrodon contortrix* shows a similar northeast to southwest trend, with a litter

---

tosiaphos kilimensis, Mabuya variata, Mochlus sundevalli, Scelotes mira, Tropidophorus brookei, Gerrhosaurus validus, Eumeces skiltonianus, Lacerta jacksoni, Latastia longicaudata, Nucras delalandii; Takydromus tachydromoides; BROOD OF FIVE—*Crotaphytus wislizenii, Holbrookia texana, Sceloporus malachiticus, Eumeces egregius, Leiolopisma zelandica, Cordylus warreni, Chamaesaura anguina, Xenosaurus grandis, Gerrhonotus coeruleus principis, G. monticola, Ameiva undulata;* BROOD OF SIX—*Crotaphytus collaris, Holbrookia maculata, Liolaemus multiformis, Sceloporus grammicus, S. ochoterenai, S. undulatus, Urosaurus ornatus, Calotes rouxi, Chalcides ocellatus, Gerrhonotus coeruleus shastensis, G. moreletii, Klauberina riversiana;* BROOD OF SEVEN—*Corytophanes percarinatus, Mabuya striata;* BROOD OF EIGHT—*Phrynosoma platyrhinos, Sceloporus occidentalis, Ichnotropis capensis;* BROOD OF NINE—*Sceloporus jarrovi, S. poinsetti, Eumeces fasciatus;* BROOD OF TEN—*Eumeces septentrionalis;* BROOD OF 11—*Sceloporus clarki, S. orcutti, Agama agama, A. cyanocephala, Chamaeleo bitaeniatus, Gerrhonotus multicarinatus;* BROOD OF 12—*Phrynosoma coronatum, Sceloporus magister, Anguis fragilis;* BROOD OF 13—*Sceloporus torquatus, Ophisaurus attenuatus;* BROOD OF 14—*Sceloporus olivaceus, Eumeces laticeps;* BROOD OF 17—*Calotes versicolor, Gerrhonotus liocephalus;* BROOD OF 18—*Phrynosoma douglassi;* BROOD OF 23—*Phrynosoma cornutum;* BROOD OF 33 (estimated)—*Ctenosaura similis;* BROOD OF 35 (estimated)—*Iguana iguana;* BROOD OF 42 (estimated)—*Tupinambis teguixin;* BROOD OF 50 (estimated)—*Varanus niloticus.* For species having broods of more than 10, the figures are only approximations since samples were small. It is shown that a brood of only two is most frequent in lizards, with numbers of species decreasing rapidly for broods with progressively larger numbers. In the histogram oviparous species are shown by heavy stippling and the letter "O"; viviparous species are shown by light stippling. The most prolific species are all oviparous.

of 6.2 in the northeastern states, 5.3 in Kansas, and 3.0 in western Texas. *Coluber constrictor* is most productive in the northeastern United States, with an average clutch of 16.8 eggs, which is reduced

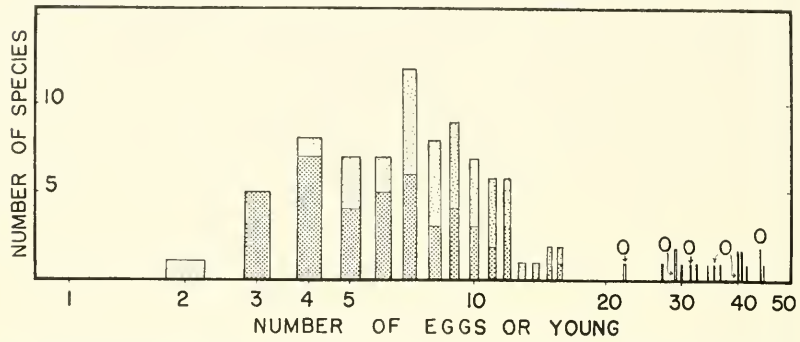


FIG. 10. Histogram showing typical size of brood (number of eggs per clutch or young per litter) in 100 species of snakes, as follows: BROOD OF TWO—*Lapemis curtus;* BROOD OF THREE—*Carphophis vermis, Tantilla coronata, Dipsas catesbyi, Opisthotropis latouchii, Microcephalophis gracilis;* BROOD OF FOUR—*Charina bottae, Diadophis punctatus, Elaphe conspicillata, Leimadophis taeniurus, Lycophidion capensis, Leptodeira annulata, Amphiesma craspedogaster, Crotalus lepidus;* BROOD OF FIVE—*Boaedon lineatus, Leimadophis reginae, Ptyas korros, Boiga multomaculata, Virginia striatula, Agkistrodon contortrix, A. halys blomhoffi;* BROOD OF SIX—*Lycodon aulicus, Philothamnus hoplogaster, Rhinocheilus lecontei, Amphiesma vibakari, Natriciteres olivacea, Crotalus pricei, Trimeresurus jerdonii;* BROOD OF SEVEN—*Masticophis lateralis, M. taeniatus, Opheodrys aestivus, O. vernalis, Oxyrhopus petolus, Natrix annularis, Seminatrix pygaea, Tropidoclonion lineatum, Virginia valeriae, Agkistrodon piscivorus, Sistrurus miliarius;* BROOD OF EIGHT—*Opheodrys major, Spalerosophis diadema, Oxyrhopus melanogenys, Storeria occipitomaculata, Agkistrodon halys, Crotalus ruber, C. scutulatus, Sistrurus catenatus;* BROOD OF NINE—*Arizona elegans, Elaphe climacophora, E. quadrivirgata, Heterodon nasicus, Thamnophis ordinoides, T. sauritus, Crotalus cerastes, Trimeresurus flavoviridis; Homalopsis buccata;* BROOD OF TEN—*Lampropeltis doliata, L. getulus, Masticophis flagellum, Clonophis kirtlandi, Thamnophis butleri, Crotalus atrox, C. horridus;* BROOD OF 11—*Lampropeltis calligaster, Psammophis subtaeniatus, Natrix fasciata clarki* (and *N. f. compressicauda*), *Regina septemvittata, Thamnophis elegans, Crotalus viridis;* BROOD OF 12—*Pituophis melanoleucus sayi, Coluber constrictor, Elaphe rufodorsatum, Ptyas mucosus, Rhabdophis tigrina, Thamnophis proximus;* BROOD OF 13—*Thamnophis marcianus;* BROOD OF 14—*Storeria dekayi;* BROOD OF 15—*Elaphe obsoleta, Thamnophis sirtalis parietalis;* BROOD OF 16—*Natrix erythrogaster, Causus rhombeatus;* BROOD OF 22—*Heterodon platyrhinos;* BROOD OF 27—*Natrix sipedon;* BROOD OF 29—*Python molurus, Thamnophis radix;* BROOD OF 30—*Vipera russellii;* BROOD OF 32—*Farancia abacura;* BROOD OF 33—*Crotalus basiliscus;* BROOD OF 35—*Eunectes murinus;* BROOD OF 36—*Farancia erytrogramma;* BROOD OF 37—*Pseudaspis cana;* BROOD OF 40—*Xenochrophis piscator, Bothrops atrox;* BROOD OF 41—*Natrix cyclopion, N. taxispilota;* BROOD OF 42—*Bitis arietans;* BROOD OF 46—*Python reticulatus, P. sebae;* BROOD OF 47—*Natrix rhombifera.* The higher numbers are estimates since few records are available for the more prolific species. It is shown that a brood of seven is modal for snakes, and that most species normally have broods in the range three to 16. In the histogram oviparous species are indicated by heavy stippling, and by the letter "O," viviparous species are indicated by light stippling, and, on the far right, by columns not designated by the letter "O." Species of snakes having small broods are mainly oviparous, and there is a tendency for the ratio of viviparous species to increase in species producing larger broods.

to 11.8 in the central states and 5.8 on the West Coast. A sample of litters of *Natrix fasciata* from inland localities averaged 31 young, whereas a smaller sample of coastal populations of eastern Florida and the Gulf of Mexico averaged only 10.5.

In the tropical African water snake, *Natriciteres olivacea*, a lowland sample had 6.3 eggs per clutch, *vs.* only 3.2 in a montane sample. *Agkistrodon halys* has a litter of 8.0 young in China and Manchuria but only 5.0 in Japan. *Lipinia noctua* has only one young at a time in the equatorial climate of New Britain, but seemingly in the Hawaiian Islands near the edge of the tropics the usual litter is two young. Accounts suggest that the African skink *Mabuya quinquetaeniata* is oviparous in the tropics but viviparous in the temperate climate of South Africa.

In almost every squamate species that has been thoroughly investigated some correlation has been found between the size (and/or age) of the productive female and the number of eggs in a clutch or young in a litter. For some of the better known species, differences in productivity between primiparous females and large old adults have been found as follows: *Crotaphytus collaris* 3.7 and 8.3, *Sceloporus horridus* 9 and 12; *S. malachiticus* 2.8 and 9; *S. olivaceus* 11.3 and 25; *S. undulatus* 5 and 8; *Eumeces fasciatus* 8.3 and 10.1; *Scincella laterale* 1.8 and 3.8; *Cnemidophorus sexlineatus* 1.8 and 4.2; *C. tigris* 2.9 and 3.9; *Lacerta muralis* 3 and 8; *Takydromus tachydromoides* 3.0 and 6.0; *Python reticulatus* 14, 15 or 16 and 96 or 103; *Coluber constrictor* 9.2 and 15.7; *Diadophis punctatus* 2.4 and 5.4; *Elaphe climacophora* 4.5 and 17.0; *E. quadrivirgata* 7.3 and 11.3; *Heterodon nasicus* 5.1 and 14.0; *Lycodon aulicus* 4.3 and 7.8; *Amphiesma vibakari* 5 and 10; *Rhabdophis tigrina* 10.9 and 16.7; *Thamnophis proximus* 6 and 17; *T. sirtalis* 12.0 and 16.4; *Agkistrodon contortrix* 3.6 and 8.7; *Trimeresurus flavoviridis* 4.4 and 11.4.

In some species the difference in productivity between young and old females is small, in others it is relatively large. It is perhaps greatest in *Python reticulatus* in which clutches of 14, 15 and 16 eggs were produced by females 10 to 11½ feet long whereas clutches of 96 and 103 were produced by females near the maximum length of 26 feet—some 2½ times the length of the small females and presumably more than 15 times their bulk, since bulk increases at a rate approximating the third power of the linear dimensions.

The potential productivity of a population of reptiles hence depends to a large extent on its age-distribution. Large and old

females not only produce larger broods, but produce them with greater consistency or at shorter intervals, so that a few such individuals may contribute more to the population than a considerably larger number of smaller, recently matured females. In the evolution of a species, the reproductive potential can be increased both by precocial attainment of sexual maturity before completion of growth, and by prolonging the growth period to permit attainment of unusual maximum size in the occasional survivors that live beyond the normal life span. It is characteristic of reptiles in general that growth continues beyond the time that sexual maturity is attained, but the tendency is much more pronounced in some. In many kinds of lizards, especially in the females, growth tapers off abruptly at a certain size, and individuals that are fully mature are remarkably uniform in length. Nevertheless, in such species, adolescence may be pushed back to a relatively early age, when females are still far short of full adult size. In temperate climates especially, such precocial maturing permits the female to contribute offspring, albeit in small numbers, to the population in the breeding season directly following that in which she herself was conceived.

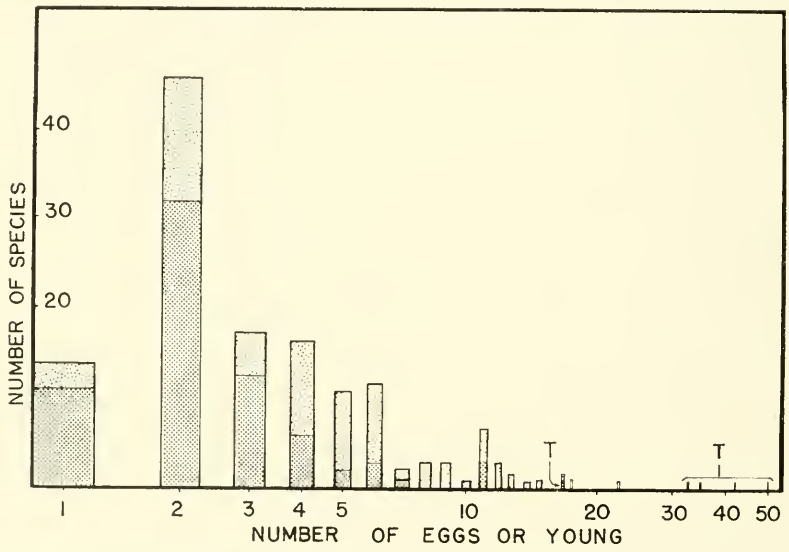


Fig. 11. Histogram showing typical size of brood in same group of species of lizards represented in Fig. 9, but segregated into tropical and subtropical species (heavy stippling or letter "T") and species of temperate climates, including the high montane of tropical regions (light stippling). The majority of species with small broods of one to three and those with large broods of more than 15 are tropical whereas species having broods of four to 15 are mostly in the Temperate Zone.

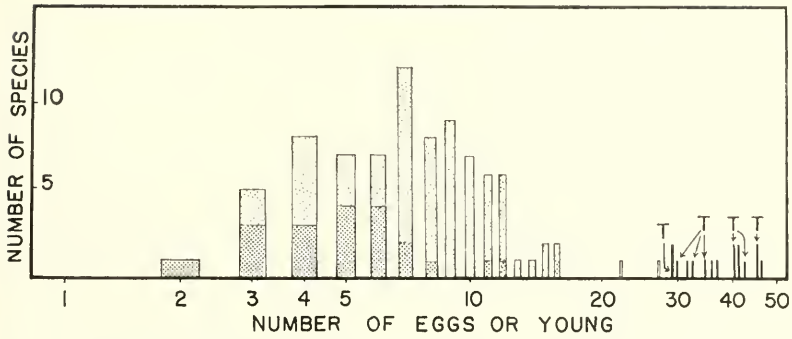


Fig. 12. Histogram showing typical size of brood in same group of snake species represented in Fig. 10, but segregated into tropical and subtropical species (heavy stippling or letter "T") and species of temperate climates, including the high montane of tropical regions (light stippling). As in lizards, the tropical species include some of the least prolific and some of the most prolific, while those with broods of intermediate sizes are best represented in the Temperate Zone.

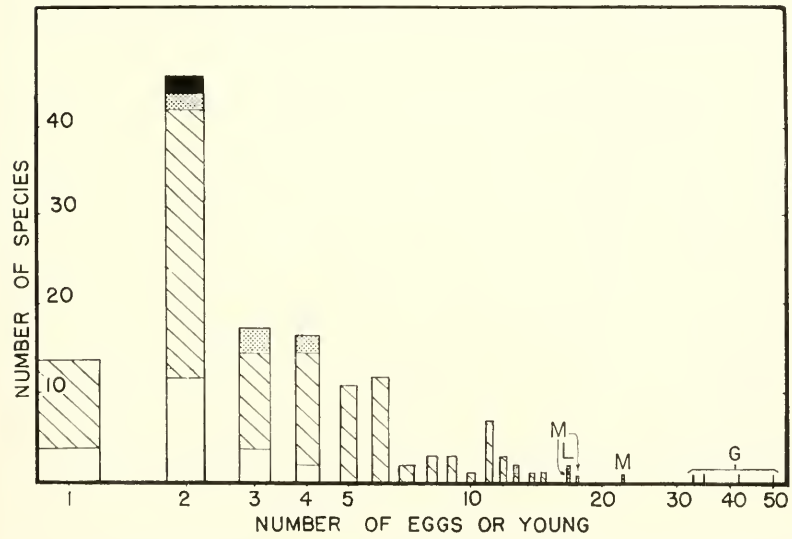


Fig. 13. Histogram showing typical size of brood in same group of species of lizards represented in Figs. 9 and 11, but here segregated into four size groups. The smallest lizards, less than two inches in snout-vent length (open columns), have broods of only one to four; those of two to five inches (diagonally barred columns and letter "M") have broods of one to 21; those over five inches and up to one foot (stippled, and letter "L") are variable; but the giant species (solid black, and letter "G") tend to be most prolific, some with broods of 30 to 50.

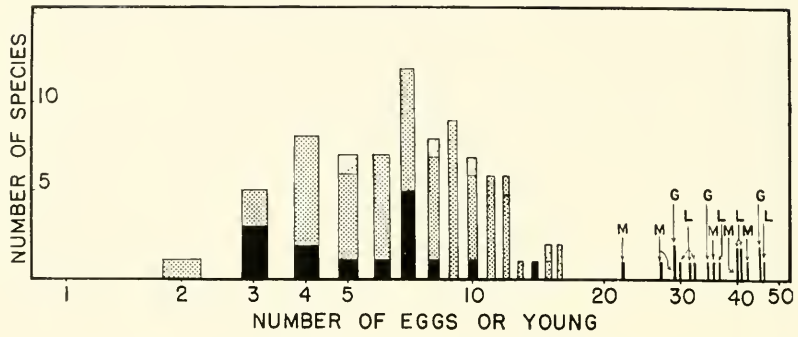


FIG. 14. Histogram showing typical size of brood in same group of species of snakes represented in Figs. 10 and 12, but here segregated into four size groups. Some correlation of number of offspring with size is shown. Small species, up to 15 inches snout-vent, are shown by solid black columns; medium-sized species, 16 inches to four feet snout-vent, are shown by heavily stippled columns and the letter "M"; large species, four to six feet snout-vent, are shown by light stippling and the letter "L"; giant species, more than six feet in snout-vent length, are indicated by the letter "G."

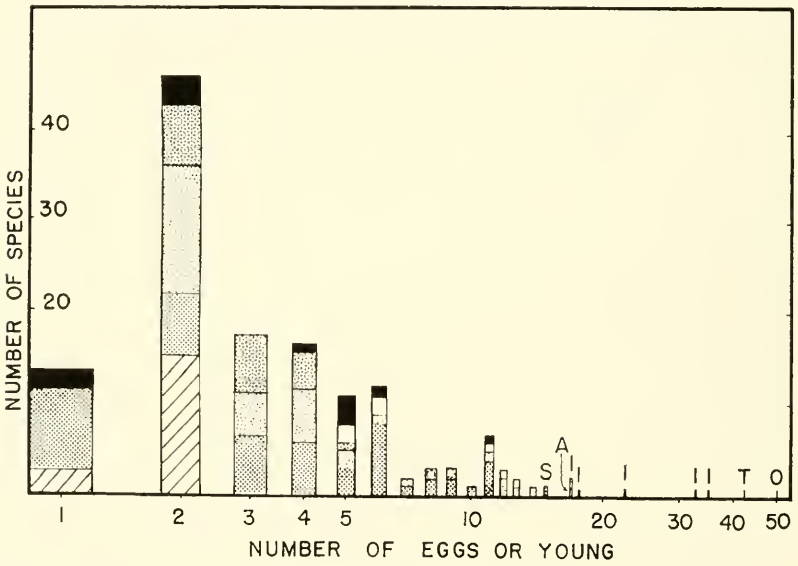


FIG. 15. Histogram showing typical size of brood in same group of species of lizards represented in Figs. 9, 11, and 13, but here segregated into six phylogenetic groups. Diagonally barred columns represent geckos, heavy stippling and letter "S" represent scincids, light stippling and letter "I" represent iguanids and agamids, circle-and-dot pattern and letter "T" represent teiids and lacertids, open columns and letter "A" represent anguids, black columns and letter "O" represent "other." Geckos produce broods of only one or two, iguanids and teiids have particularly wide ranges in sizes of broods, and anguids tend to be relatively prolific as compared with most other groups.

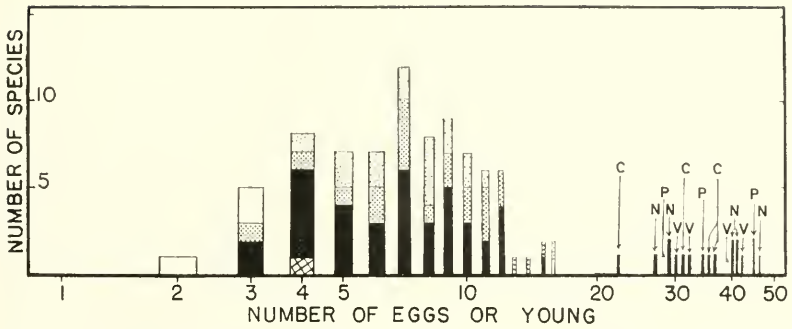


Fig. 16. Histogram showing typical size of brood in same group of species of snakes represented in Figs. 10, 12, and 14, but here segregated into five groups according to relationships, as follows: pythons and boas indicated by cross-hatched column and letter "P"; colubrid (nonmatricine) represented by solid black columns and letter "C"; matricines represented by heavily stippled columns and letter "N"; viperids and crotalids represented by light stippling and letter "V"; "others" represented by open columns. The most prolific species of snakes are largely matricines, vipers, and giant constrictors but with a few colubrids. The colubrids are especially well represented among those species having from three to ten offspring.

Timing of Breeding Seasons

Geographic area and the climate are obvious determining factors for the patterns of reproductive cycles. In the cooler parts of the Temperate Zone there is invariably a short and well-defined breeding season in spring (but in some species copulation may also occur in autumn before entrance into hibernation), ovulation later in spring, and birth of young or hatching of eggs in late summer and/or early autumn. In some of the more northern kinds, the female may ovulate only biennially, or at even longer intervals in the adder *(Vipera berus)* of northern Europe. In the mid-Temperate zones the breeding season is longer and various kinds of oviparous lizards produce up to five or six clutches per season. Typical examples of such lizards having multiple clutches in the course of a long breeding season are *Coleonyx, Anolis, Callisaurus, Crotaphytus, Holbrookia, Sceloporus ,Uma, Urosaurus, Uta, Agama, Sitana, Carlia, Emoia, Scincella, Cnemidophorus, Eremias, Lacerta, Ophisops, Takydromus,* and *Gerrhonotus.* For snakes living in similar climates, one clutch per season seems to be the general rule. But various species of snakes in the Temperate Zone are known to have somewhat lengthened breeding seasons, suggesting the possibility of more than one brood being produced, although in most instances this has not been definitely proven. These include *Diadophis punctatus, Heterodon nasicus, H. platyrhinos, Opheodrys*

aestivus, Salvadora hexalepis, Natrix cyclopion, Natrix sipedon, Regina alleni, R. septemvittata, Seminatrix pygaea, Storeria dekayi, S. occipitomaculata, and others.

Four species of Temperate Zone snakes have each been known to produce two broods in the course of a season. For one of these, *Pituophis melanoleucus,* intervals between first and second clutches were 42, 53, and 53 days. For another, *Spalerosophis diadema* the interval was 97 days. The remaining two species are both viviparous; in *Thamnophis proximus* intervals of 91 and 95 days between litters have been recorded, and for *T. sauritus* an interval of about 14 weeks.

On the other hand, in various species of snakes of the Temperate Zone, which supposedly have annual breeding cycles, population samples include varying numbers of adult and seemingly normal females which are unproductive; at least they are not gravid at the time when most other adult females contain eggs or embryos. The proportion of such nonbreeders differs according to the age- and size-group of the snakes involved. For instance, in a sample of 46 adult female racers from Kansas in the breeding season, the following were nonbreeders: probable two-year-olds, 86 per cent; three-year-olds, 44 per cent; four-year-olds, 40 per cent; five-year-olds, 43 per cent; six-year-olds and older, 20 per cent. In a sample of 181 adult females of *Thamnophis sirtalis* from the same region, percentages of nonbreeders were: two-year-olds, 58 per cent; three-year-olds, 42 per cent; four-year-olds, 6½ per cent; five-year-olds, 17 per cent and six-year-olds, none. In these instances actual ages of the individual females usually were not known but were extrapolated from their sizes and from known average growth rates. Obviously size and age are only two of many factors which affect productivity. Nutrition certainly is important also. For reasons that were not evident, in several instances individual females *(e.g. Pituophis melanoleucus, Leptodeira annulata)* which were kept in captivity and thrived and usually produced clutches at approximately annual intervals occasionally missed a year. In several lizards of xeric habitats, including *Xantusia vigilis, Uma inornata, U. scoparia, Uta stansburiana,* and *Sceloporus orcutti,* productivity during the annual breeding season is demonstrably correlated with the amount and distribution of rainfall, presumably through its effect on the vegetation and on the insect population that it supports. Both male and female reproductive cycles may be partly or wholly suppressed in years of inadequate precipitation.

In warm-temperate and subtropical regions breeding seasons tend to be lengthened, and in some instances are timed with reference to the seasonal distribution of rainfall rather than to the annual temperature cycle. In drier parts of the tropics breeding seasons tend to be limited to the time of year when there is maximum rainfall. In tropical and subtropical regions relatively few of the reptiles that have been studied have been shown to have short and well-defined breeding seasons. However, seemingly most of the hydrophiids do fall in this category; perhaps the king cobra *(Ophiophagus)*, the north Australian taipan *(Oxyuranus)*, and the African puff adder *(Bitis arietans)* do also. Among nonvenomous snakes *Adelophis veraepacis*, *Alsophis angulifer*, and *Dendrelaphis punctulatus*, insofar as known, limit their breeding to certain parts of the year, and the same is true of the equatorial marine iguana *(Amblyrhynchus cristatus)*, of the montane iguanid *Liolaemus multiformis* of southern Perú, and of the iguanas, *Iguana* and *Ctenosaura* in Central America and *Cyclura* in the West Indies, *Chamaeleo melleri* and some closely related species of chameleons in tropical Africa, and perhaps species of *Varanus*. Most other tropical and subtropical species that have been well investigated have proved to have extended breeding seasons, which in some instances last throughout the year. This applies to many tropical geckos, to anoles, various agamids and chameleons, skinks, lacertids and teiids. Also it applies to the snakes, *Dendrelaphis tristis, Calamaria lumbricoidea, C. linnaei, Dryomoluber dichrous, Duberria lutrix, Elapoides fuscus, Gongylosoma baliodeira, Leptophis ahaetulla, Lycodon aulicus, Lycophidion capensis, Ninia maculata, N. sebae, Philothamnus hoplogaster, P. irregularis, P. semivariegatus, Prosymna ambigua, Ptyas korros, P. mucosus, Xenodon severus, Amphiesma stolata, Aspidura trachyprocta, Atretium schistosum, Macropisthodon plumbicolor, Natriciteres olivacea, Natrix trianguligera, Pseudoxenodon macrops, Rhabdophis chrysarga, R. subminiata, Xenochrophis cerasogaster, X. piscator, X. vittata, Boiga ceylonensis, B. trigonatus, B. multomaculata, Crotaphopeltis hotamboeia, Ahaetulla nasuta, Imantodes cenchoa, Leptodeira maculata, L. annulata, L. septentrionalis, Oxyrhopus petolus, Psammophis pulverulentus, Oxyrhopus melanogenys, Trimorphodon biscutatus, Dipsas catesbyi, Enhydris enhydris, E. plumbea, Dasypeltis scabra* and *Vipera russellii.*

Even in tropical snakes relatively few specific instances of repeated layings by an individual female within a season have been

reported although presumably this is a regular occurrence in many species. Some actual records of intervals between successive clutches are: 10 weeks in *Boaedon lineatus*, 60 days in *Boiga multomaculata*, approximately 30 days in *Causus rhombeatus*, 59 days in *Ptyas mucosus*, 70 days in *P. korros*, 41 days in *Xenochrophis vittata*, and 44 days in *Rhabdophis subminiata*.

Viviparity versus Oviparity

One of the factors which makes for diversity in reproductive cycles in the Squamata is this group's vacillation between the oviparous and viviparous conditions. Primitively the squamates are oviparous, producing large-yolked eggs which can survive only in moist surroundings and which require several weeks, or sometimes several months, to develop. However many squamate families and genera have independently evolved in the direction of viviparity, by retaining the fertilized eggs in the oviducts during their embryonic development, and by achieving structures of varying degrees of complexity for the transfer of materials between the mother and her developing offspring.

In the foregoing species' accounts there are cited instances in which normally oviparous kinds of reptiles retained eggs in their oviducts until embryonic development was completed, and then gave birth to living young. Hence the attainment of viviparity seems an easy step in evolution. Yet despite the seeming trend toward viviparity, a large majority of snakes and lizards have retained oviparous habits and viviparity has developed only under special conditions that render it advantageous. Certainly viviparity is not necessarily the best and most efficient means of reproduction in all situations; oviparity and viviparity each impose certain special limitations as well as conferring certain special benefits. Presumably, in the course of evolution the transition from oviparity to viviparity is a step that is not readily reversible. Nevertheless, a species that had become viviparous only recently in its evolutionary history and had not greatly altered its gene balance for such adjustments as the production of eggshell, might conceivably retain the potentiality to revert to the oviparous state when such a change would be advantageous.

Oviparity and viviparity are closely linked with reproductive potentials. Oviparous reptiles tend to be more prolific because when the female has oviposited she may be able to produce another clutch in a relatively short time. The following are a few specific

examples of intervals between clutches, including both averages and isolated instances: 17.5 days in *Takydromus tachydromoides*, 19 days in *Sitana ponticeriana*, 20 days in *Sceloporus undulatus* and *Eublepharis macularius*, 21± days in *Crotaphytus collaris*, 22 days in *Scincella laterale*, 24 days in *Sceloporus olivaceus*, 25 days in *Gerrhonotus infernalis*, 30 days in *Uma notata*, 30± days in *Holbrookia texana*. In snakes the minimum reported interval seems to be 26 days in *Causus rhombeatus*.

In viviparous species the female is gravid for a much longer time, and is usually more debilitated after parturition than is an oviparous female that has just oviposited. Hence the interval between successive ovulatory periods is long—most typically a year and sometimes two years or several. In *Thamnophis proximus*, *T. sauritus*, *Sceloporus malachiticus*, and certain chameleons, the females seemingly have the capacity under favorable conditions to ovulate again soon after the birth of a litter, but presumably there are relatively few live-bearers that have this capacity. In live-bearers not only are all the eggs "in the same basket" but the "basket" is the female who is considerably burdened and handicapped against an oviparous competitor and also made vulnerable to natural enemies or other mortality factors. The female is severely handicapped in such activities as swimming, digging, running or climbing, sometimes to the extent that she ceases to feed and remains inactive in sheltered situations, surviving and sustaining her developing young by drawing upon reserves of stored fat. The filling of the female's body cavity by the growing embryos also may make it difficult for her to ingest or digest sizable food items.

Compensatory advantages that accrue from viviparity include: 1. Emancipation from the necessity of digging, or finding, a suitable nest burrow—a necessity which may have limited the oviparous counterpart to soils of a certain mechanical consistency and chemical composition and a certain range of moisture content. 2. Protection of the eggs from harmful growths of mold or bacteria. 3. Protection of the eggs from invertebrates such as ants, beetles or fly larvae, which might feed upon them. 4. Protection of eggs from small vertebrate predators which can be repulsed by the gravid female. 5. Protection of eggs from large predators, which can be escaped by speed or elusiveness, or, in some instances, may be repulsed or intimidated, especially by the females of venomous species. 6. Ability to transport the eggs and "juggle" them between different microhabitats, thus avoiding unfavorable or lethal ex-

tremes of temperature and/or moisture, but taking advantage of the most favorable aspects of the general environment at any one time. This last advantage applies especially in far northern and alpine and certain coastal climates where environmental temperatures, especially those beneath the soil surface are usually too low to permit effective incubation of eggs.

Hence in viviparity, the chances of any one egg completing its embryonic development are increased, but the female's life expectancy is shortened by the stresses and handicaps of pregnancy. As a general rule, however, those forms which are viviparous have relatively long life expectancy; viviparity would not be advantageous to a species if the female's chances of surviving pregnancy were low. The advantage of viviparity applies particularly to highly aquatic kinds, and those specialized for arboreal existence to the degree that they cannot venture to the ground without undue risk, and have little or no capacity for digging.

In the cooler parts of the Temperate zones, where reptiles are able to exist, the number of species represented is small, and a high proportion of them, but not all, are viviparous. In different parts of the world some of the groups that range farthest from the equator are the viperids, crotalids, natricines, colubrines, iguanids, gekkonids, anguids and scincids. In progressively warmer climates the total number of species and the proportion of egg-layers rapidly increases.

Viviparity is also correlated with the body form and life habits of the animal itself. Those kinds which are of stout, squat and chunky build and are normally slow-moving or secretive, can assume viviparity without much loss. But for slender, streamlined species which habitually depend on speed and agility to catch their prey and to escape enemies, the handicap involved in a long pregnancy might be too great to permit a shift to viviparous habits.

In his able discussion of viviparity in snakes, Neill (1964b:41) emphasized the factor of protection afforded the embryos by the gravid females of venomous types, and credited to this factor the prevalence of viviparity in vipers and pit vipers and other venomous groups. Undoubtedly the protection afforded by the venomous female is a real factor. But in evaluating it one must explain the frequent occurrence of viviparity in lizards and in nonvenomous snakes and the fact that many kinds of dangerously venomous snakes, even some of the vipers and pit vipers, have retained oviparous habits. Snakes of the genera *Agkistrodon, Bitis, Bothrops,*

Crotalus, Trimeresurus, and *Vipera* are typical of viviparous reptiles in general in their chunky bodies, sluggish habits and cryptic coloration, enabling them to escape notice of their enemies and to ambush their prey with a minimum of activity. The same applies to the viperlike Australian elapid death adder *(Acanthophis)* and to a lesser degree to the tiger snake *(Notechis).* Among other Australian elapids there are additional genera also that are viviparous and are rather stout-bodied, but the slender whiplike, highly active genera *(Demansia, Oxyuranus, Pseudonaja)* are all oviparous.

As an explanation of viviparity in many of the Australian elapids, adaptation to extreme xeric conditions (Weekes, 1935) seems at least equally as plausible as the supposition that this condition was acquired for protection of the unborn young from natural enemies. Although the Australian varanids, geckos, and agamids, living under similarly xeric conditions, all have remained oviparous, these are mostly active, fast-moving lizards and many of the skinks, especially heavy-bodied forms and those that are highly scretive, have become viviparous *(Egernia, Hemiergis, Sphenomorphus, Tiliqua, Trachydosaurus).*

In reviewing further the incidence of viviparity in snakes and lizards it should be noted that there are only a few important groups that are exclusively viviparous. These include annielids (a small group, living in part in a cool coastal climate), cordylids (armored, and generally slow-moving, lizards usually living in well protected situations such as rock crevices, and some of them occuring in cool-temperate climate), xantusiids and xenosaurids (small groups of somewhat secretive lizards, again living in well sheltered situations), boas (sluggish, stout-bodied snakes, some occurring in cool climates), acrochordids, homalopsine colubrids and hydrophiines (groups highly specialized for marine life, or at least having well-developed aquatic adaptations).

The remaining viviparous snakes and lizards all belong to families or subfamilies that are partly oviparous, but may be divided into those groups in which viviparity is common and those in which it is exceptional. In the first category come the crotalids, viperids, and elapids, already discussed. Outside of Australia the only viviparous elapid is the spitting cobra of South Africa, *Haemachatus,* a rather stout and heavy snake compared with the numerous oviparous elapids of Asia, Africa and the Neotropical region. The natricines show an even sharper geographical dichotomy than the elapids, since all the genera and species of the New World are

viviparous, whereas the diverse Old World representatives are all oviparous with the single exception of *Natrix annularis*. Although the New World representatives are fairly diverse, a possible explanation for their uniform viviparity is that all are derived from the common ancestry of a northern viviparous species of *Natrix*. Actually, the American natricines as a group are relatively northern in their distribution, while the widely distributed Old World counterparts have a much higher proportion of tropical and subtropical species. The Anguidae and Scincidae are the only other large families in which viviparity is common. In some instances this may be in adaptation to a cool climate as in a northern or montane habitat *(Anguis, Abronia, Gerrhonotus)* but in many other instances the lizards involved are tropical. Secretiveness, partly subterranean life, and the habit of living in dense ground cover such as leaf litter, or decaying wood, or in rock crevices, seem typical of these lizards. Some of them are slow and heavy-bodied, and they show varying amounts of body armor.

In the remaining groups of snakes and lizards the viviparous species are the relatively rare exceptions that have acquired such habits in obvious adaptation to special conditions. In the geckos for instance, oviparity is the rule and the New Zealand representatives that have become viviparous occur in relatively cold climates, with incidentally, unusually few efficient predators. In the Iguanidae viviparity has become established in the high montane species of *Liolaemus*, and *Corytophanes*, in various species of *Sceloporus*, and in certain horned lizards, *Phrynosoma*. In *Sceloporus*, the viviparous species are in the minority, but occur in at least four different groups within the genus, and obviously the evolutionary transition from oviparity to viviparity has occurred several times. Although some of the viviparous sceloporine species are montane others are instead more characteristic of xeric situations. In general it seems that the viviparous species are stout-bodied, and are saxicolous or at least occur in situations with readily available shelter—in contrast to the oviparous types, some of which are ground-living and cursorial. In the horned lizards, *Phrynosoma*, most species are oviparous. The closely related *P. douglassi* and *P. orbiculare* are both viviparous, and are montane and/or northern in relation to the distribution of other species. The sluggish behavior, squat form, cryptic coloration and myrmecophagous habits of horned lizards are typical of viviparous reptiles, but it is noteworthy that the agamid counterpart, the Australian

moloch, is oviparous. In the agamids, viviparity appears only in the slow-moving arboreal *Cophotis* and perhaps in the squat, heavy-bodied desert-living *Phrynocephalus* which conceals itself in burrows or loose sand. Among the chameleons the viviparous species are, in general, those that live at high altitudes and those in South Africa, farthest from the equator. In the Lacertidae, only *Lacerta vivipara* notable for its far northern distribution, is viviparous. Among colubrine snakes oviparity is the rule but with occasional viviparous forms. The viviparous *Ahaetulla* is highly specialized for arboreal existence. Despite their slender attenuate body form, these snakes are described as slow-moving, and seemingly they hunt by ambush. In *Psammodynastes,* another viviparous Old World opisthoglyph and in a group of several rear-fanged South American genera the significance of viviparity is problematical. Viviparity in *Coronella austriaca* and *Elaphe rufodorsata* is probably linked with their relatively northern distribution. The South African slug-eating *Duberria* also occurs in relatively cool climates, and in South America the highly aquatic *Helicops* is the only known viviparous aglyphous colubrine. The Central American *Conopsis* and *Toluca* obviously have become viviparous in response to high montane habitats.

The habit of brooding is an alternative, or perhaps a substitute, for viviparity, and confers some of the same advantages and handicaps. Many of the kinds of reptiles that have been reported to brood lay their eggs with embryos already partly developed and some have close relatives that are viviparous. However, relatively few genera and species are known to brood. In lizards, especially, brooding seems to be confined to certain groups—anguids (*Gerrhonotus liocephalus, Diploglossus bilobatus, D. delasagra, Ophisaurus* several species) and scincids (*Eumeces* probably all the oviparous species, possibly *Emoia*)—of secretive habits, in which olfaction is important, and the role of olfaction in maintaining the female's interest in her eggs has been well demonstrated.

In snakes the relatively few kinds reported to brood are remarkably diverse in size, habits, and relationships, and include: typhlopids (*?, Typhlops avakubae*), leptotyphlopids (*Leptotyphlops dulcis*), pythons (*Python curtus, P. molurus, P. reticulatus, P. sebae, Liasis amethistinus*), elapids (*Bungarus caeruleus, Naja naja, Ophiophagus hannah,* perhaps *Micrurus corallinus*), crotalids (*Agkistrodon rhodostoma, Trimeresurus monticola*), opisthoglyphous colubrines (*Psammophylax rhombeatus*), aglyphous colubrines (*Elaphe climaco-*

phora, E. quadrivirgata, Farancia abacura, Ptyas korros), and probably at least one natricine *(Opisthotropis latouchii).* Male brooding has been reported but not well substantiated in *Naja naja* (male accompanying the brooding female) and *Diploglossus delasagra* (male alone attending nest). However, brooding is primarily a female function. In some species the female's affinity for the eggs is strong, and she remains closely associated with them throughout their incubation. In other species brooding may occur only occasionally, or may be confined to the early part of the incubation period, or the female may be inclined to abandon the eggs at any disturbance.

Obviously the brooding habit has evolved independently many times in reptiles, and perhaps it serves different needs. Brooding has been studied most thoroughly in the pythons, and in these giant snakes it is well established that an important function of the female is to raise the temperature of the eggs and hasten their incubation. However, careful study of incubation in skinks of the genus *Eumeces* has indicated that there is little or no regulation of temperature by the brooding female, but that her regulation of moisture in the nest is an important function. In the dangerously venomous snakes, *Psammophylax, Micrurus, Bungarus, Naja, Ophiophagus, Agkistrodon,* and *Trimeresurus,* guarding and defending of the eggs is of obvious value. The female of *Opisthotropis latouchii,* having the habit of laying her eggs under flat rocks at the edges of mountain streams, could conceivably compensate for rising or falling water level by shifting the eggs to keep them from becoming too dry or too wet, but it is not known whether incubation is of regular occurrence in this genus.

In *Gerrhonotus liocephalus* and *Ptyas korros* the observed brooding habits are somewhat incongruous with the fact that females are known to produce successive clutches. A female that remained inactive guarding her eggs after ovipositing would probably lack sufficient energy and food material to produce another clutch. However, it is not known how well the brooding habit is established in these species, or whether the females that produce second clutches are individuals that have lost or abandoned their original clutches.

LITERATURE CITED

Alcala, A. C., and W. C. Brown
1967. Population ecology of the tropical scincoid lizard, *Emoia atrocostata*, in the Philippines. Copeia, 1967(3):596-604.

Allen, E. R.
1939. Habits of *Rhadinea flavilata*. Copeia, 1939(3):175.

Allen, E. R., and D. Swindell
1948. Cottonmouth moccasin of Florida. Herpetologica, 4(first supl.):1-16.

Allen, W. B., Jr.
1955. Some notes on reptiles. Herpetologica, 11:228.

Alvarez del Toro, M.
1960. Reptiles de Chiapas. Inst. Zool. del Estado, Tuxtla Gutiérrez, Chiapas, 204 pp.

Amaral, A. do
1921. Seccao de Ofiologia. Biology of the new species, *Lachesis insularis*. Pp. 85-88 *in* Anexos das Memórias do Instituto Butantan, vol. 1, Fasc. 1, 90 pp.
1926. Sobre *Lachesis muta* Daudin, 1803, espécie ovípara. Collectana Ofiologica, São Paulo.
1927. Contribuição à biologia dos ofídios brasileiros (reprodução). Col. Trab. Inst. Butantan, 2:185-187.

Amrein, Y. U., and M. B. Amrein
1951. The number of young found in the island night lizard. Copeia, 1951(2):180.

Anderson, J. D.
1962. Egg laying and nesting in *Sceloporus scalaris slevini*. Herpetologica, 18(3):162-164.

Anderson, P.
1942. Amphibians and reptiles of Jackson County, Missouri. Bull. Chicago Acad. Sci., 6(11):203-220.
1965. The reptiles of Missouri. Univ. Missouri Press, Columbia, Missouri, xxiii + 330 pp.

Anderson, S. C.
1963. Amphibians and reptiles from Iran. Proc. California Acad. Sci., fourth series, 31(16):417-498.

Angel, F., J. Guibé, M. Lamotte, and R. Roy
1954. La réserve naturelle intégrale du Mont Nimba. Mem. Inst. Français d'Afrique noire. No. 40, II, Serpents, pp. 381-402.

Asana, J. J.
1931. The natural life history of *Calotes versicolor* (Boulenger) the common blood-sucker. Jour. Bombay Nat. Hist. Soc., 34:1041-1047.

Asplund, K. K., and C. H. Lowe
1964. Reproductive cycles of the iguanid lizards, *Urosaurus ornatus* and *Uta stansburiana* in southeastern Arizona. Jour. Morph., 115:27-33.

Atsatt, S. R.
1952. Observations on the early life history of the lizards *Sceloporus graciosus vandenburgianus* and *Gerrhonotus multicarinatus webbi*. Copeia, 1952(4):276.
1953. Storage of sperm in the female chameleon, *Microsaura pumila pumila*. Copeia, 1953(1):59.

Axtell, R. W.
1956. A solution to the long neglected *Holbrookia lacerata* problem, and the description of two new subspecies of *Holbrookia*. Bull. Chicago Acad. Sci., 10(11):163-179.
1959. Amphibians and reptiles of the Black Gap Wildlife Management Area, Brewster County, Texas. Southwestern Nat., 4(2):88-109.
1960. A new subspecies of *Eumeces dicei* from the Sierra Madre of northeastern Mexico. Copeia, 1960(1):19-26.

Babbitt, L. H.
1951. Courtship and mating of *Eumeces egregius*. Copeia, 1951(1):79.

Bailey, J. R.
1966. A redescription of the snake *Calamodontophis paucidens*. Copeia, 1966(4):885-886.
Baker, J. R.
1947. The seasons in a tropical rain-forest. Part 6. Lizards *(Emoia)*. Jour. Linn. Soc. London, 41(no. 279):243-247.
Barbour, R. W.
1960. A study of the worm snake, *Carphophis amoenus* Say, in Kentucky. Trans. Kentucky Acad. Sci., 21(1/2):10-16.
Barbour, T.
1937. Ovoviviparity in *Trachyboa*. Copeia, 1937(2):139.
Bartholomew, G. A., Jr.
1953. The modification by temperature of the photoperiodic control of gonadal development in the lizard *Xantusia vigilis*. Copeia, 1953 (1):45-50.
1966. A field study of temperature relations in the Galapagos marine iguana. Copeia, 1966:241-250.
Barton, A. J.
1952. A new size record for the eastern gartersnake, *Thamnophis sirtalis sirtalis* (Linnaeus). Copeia, 1952(3):190-191.
Barwick, R. E.
1959. The life history of the common New Zealand skink *Leiolopisma zelandica* (Gray, 1843). Trans. Royal Soc. New Zealand, 86(3-4): 331-380.
Bechtel, H. B., and E. Bechtel
1958. Reproduction in captive corn snakes, *Elaphe guttata guttata*. Copeia, 1958(2):148-149.
1962. Heredity of albinism in the corn snake, *Elaphe guttata guttata*, demonstrated in captive breedings. Copeia, 1962(2):436-437.
Beebe, W.
1944. Field notes on the lizards of Kartabo, British Guiana, and Caripito, Venezuela. Part 1, Gekkonidae. Zoologica, 29:145-160. Part 2, Iguanidae. Zoologica, 29(4):195-216.
1945. Part 3, Teiidae, Amphisbaenidae and Scincidae. Zoologica, 30:7-32.
1946. Field notes on the snakes of Kartabo, British Guiana and Caripito, Venezuela. Zoologica, 31:11-52.
Bellis, E. D.
1964. A summer six-lined racerunner *(Cnemidophorus sexlineatus)* population in South Carolina. Herpetologica, 20(1):9-16.
Belluomini, H. E., and A. R. Hoge
1958. Operação cesariana realizada em Eunectes murinus (Linnaeus, 1758) (Serpentes). Mem. Inst. Butantan, 28:187-194.
Bergman, A. M.
1943. The breeding habits of sea snakes. Copeia, 1943(3):156-160.
Bergman, R. A.
1963. The anatomy of *Ablabes baliodeira*, a colubrid snake from Java. Jour. Ohio Herp. Soc. 4(12):1-14.
Berry, P. Y., and C. S. Lim
1967. The breeding pattern of the puff-faced water snake, *Homalopsis buccata* Boulenger. Copeia, 1967(2):307-313.
Betz, T. W.
1963a. The gross ovarian morphology of the diamond-backed water snake, *Natrix rhombifera*, during the reproductive cycle. Copeia, 1963(4): 692-697.
1963b. Neonatal *Natrix cyclopion floridana*. Copeia 1963(3):575-576.
Bishop, M. B.
1940. Notes concerning two broods of young of *Natrix compressicauda*. Copeia, 1940(2):128.
Blackwell, K.
1952. Notes on the viperine snake *(Natrix maura)*. British Jour. Herp., 1(7):134-136.

1954. Some notes on the egg-laying, and retention of the spermatozoa by the African snake, *Boaedon lineatus*. British Jour. Herp., 1(10): 189-190.

Blair, A. P.
1961. Notes on *Ophisaurus attenuatus attenuatus* (Anguidae). Southwestern Nat., 6:201.

Blair, W. F.
1960. The rusty lizard, a population study. University of Texas Press, Austin, xvi + 185 pp.

Blanchard, F. N.
1921. A revision of the king snakes: genus *Lampropeltis*. Bull. U.S. Nat. Mus., 114:iv + 260 pp.
1930. Further studies of the eggs and young of the eastern ringneck snake, *Diadophis punctatus edwardsii*. Bull. Antevenin Inst. of America, 4(1):4-10.
1933. Eggs and young of the smooth green snake *Opheodrys vernalis* (Harlan). Papers Michigan Acad. Sci. Arts and Letters, 17:493-508.
1936. Eggs and natural nests of the eastern ringneck snake, *Diadophis punctatus edwardsii*. Papers Michigan Acad. Sci. Arts and Letters, 22:521-532.
1937. Data on the natural history of the red-bellied snake, *Storeria occipito-maculata* (Storer), in northern Michigan. Copeia, 1937(3): 151-162.

Blanchard, F. N., and E. R. Force
1930. The age of attainment of sexual maturity in the lined snake, *Tropidoclonion lineatum* (Hallowell). Bull. Antevenin Inst. America, 3(4):96-99.

Blanford, W. T.
1876. On some of the specific identifications in Dr. Günther's Second Report on collections of Indian reptiles obtained by the British Museum. Proc. Zool. Soc. London, 1876:635-637.

Blount, R. F.
1929. Seasonal cycles of the interstitial cells in the testis of the horned toad *(Phrynosoma solare)*. Jour. Morph., 48:317-343.

Bogdanov, O. P.
1966. [The distribution and ecology of the central Asian cobra *Naja oxiana* (Eichwald)]. *In* [Problems of the herpetology and toxicology of snake venoms]. Nauka: Tashkent. 5-9. (In Russian)

Bogert, C. M.
1940. Herpetological results of the Vernay Angola Expedition with notes on African reptiles in other collections. Bull. Amer. Mus. Nat. Hist., 77:1-107, 1 pl.

Bogert, C. M., and R. M. del Campo
1956. The Gila monster and its allies. The relationships and behavior of the lizards of the family Helodermatidae. Bull. Amer. Mus. Nat. Hist., 109, article 1, 238 pp.

Bons, J.
1964. Note sur la ponte du lézard *Agama bibroni* (Sauria, Agamidae). Bull. Soc. Sci. Nat. Phys. Maroc., 44:65-71.

Bons, J., and N. Bons
1960. Notes sur la reproduction et le développement de *Chamaeleo chamaeleon* L. Bull. Soc. Sci. Nat. et Phys. Maroc., 40(4):323-335.

Bons, J., and H. Saint-Girons
1963. Ecologie et cycle sexuel des Amphisbeniens du Maroc. Bull. Soc. Sci. Nat. Phys. Maroc., 43(3/4):117-158.

Bostic, D. L.
1966. A preliminary report of reproduction in the teiid lizard, *Cnemidophorus hyperythrus beldingi*. Herpetologica, 22(2):81-90.

Bothner, R. C., and T. R. Moore
1964. A collection of *Haldea valeriae pulchra* from western Pennsylvania, with notes on some litters of their young. Copeia, 1964(4):709-710.

Boyer, D. A., and O. A. Heinze
1934. An annotated list of the amphibians and reptiles of Jefferson County, Missouri. Trans. St. Louis Acad. Sci., 28:183-200.
Brain, C. K.
1959a. Note on the breeding of the South African skink, *Typhlosaurus lineatus* Boulenger. Copeia, 1959(1):70-71.
1959b. Mating in the South African mole snake, *Pseudaspis cana* (Linnaeus). Copeia, 1959(1):71-72.
Brattstrom, B. H.
1951. The number of young in *Xantusia*. Herpetologica, 7(3):143-144.
1953. Notes on a population of leaf-nosed snakes *Phyllorhynchus decurtatus perkinsi*. Herpetologica, 9(2):57-64.
Brattstrom, B. H., and T. R. Howell
1954. Notes on some collections of reptiles and amphibians from Nicaragua. Herpetologica, 10(2):114-123.
Breckenridge, W. J.
1943. The life history of the black-banded skink, *Eumeces septentrionalis septentrionalis* (Baird). Amer. Midl. Nat., 29:591-606.
Breder, C. M.
1946. Amphibians and reptiles of the Rio Chucunaque drainage, Darien, Panama, with notes on their life histories and habits. Bull. Amer. Mus. Nat. Hist., 86(8):381-435.
Brimley, C. S.
1903. Notes on the reproduction of certain reptiles. Amer. Nat., 37:261-264, 266.
Broadley, D. G.
1959. The herpetology of southern Rhodesia. Part 1, Snakes. Bull. Mus. Comp. Zool., 120(1):1-100.
Brongersma, L. D.
1942. Notes on scincid lizards. Zool. Med., 24(1-2):126-152.
Brooks, G. R., Jr.
1967. Population ecology of the ground skink, *Lygosoma laterale* (Say). Ecol. Mongr., 37(2):71-87.
Brown, B. C.
1937. Notes on *Coniophanes imperialis* (Baird). Copeia, 1937:234.
Brown, E. E.
1956. Nests and young of the six-lined racerunner *Cnemidophorus sexlineatus* Linnaeus. Jour. Elisha Mitchell Sci. Soc., 72(1):30-40.
Bundy, R. E., D. Meyer, and J. Neess
1955. Observations on two species of lizards in the Chihuahuan Desert. Copeia, 1955(4):312.
Burger, W. L., and J. E. Werler
1954. The subspecies of the ring-necked coffee snake, *Ninia diademata*, and a short biological and taxonomic account of the genus. Univ. Kansas Sci. Bull., 36(2), no. 10:643-672.
Burkett, R. D.
1962. Two clutches of eggs in the lizard, *Gerrhonotus liocephalus infernalis*. Herpetologica, 18(3):211.
1966. Natural history of the cottonmouth moccasin, *Agkistrodon piscivorus* (Reptilia). Univ. Kansas Publ. Mus. Nat. Hist., 17(9):435-491.
Burrage, B. R.
1965. Notes on the eggs and young of the lizards *Gerrhonotus multicarinatus webbi* and *G. m. nauus*. Copeia, 1965(4):512.
Burt, C. E.
1935. Notes on a collection of lizards from western Mexico and tropical America. Trans. Micr. Soc., 54(2):167-178.
Burt, C. E., and W. L. Hoyle
1934. Additional records of reptiles of the central prairie region of the United States. Trans. Kansas Acad. Sci., 37:193-216.
Busack, S. D., and L. D. Busack
1967. Notes on the growth rate of *Microsaura pumila pumila* (Lacertilia: Chamaeleontidae). Herpetologica 23(3):231-232.

Bustard, H. R.
1955. Observations on the birth of two species of lizards in the vivarium. British Jour. Herp., 2(1):6-9.
1957. Observations on zonures and geckos in captivity. British Jour. Herp., 2(4):71-75.
1961. Birth of the lizard *Sceloporus cyanogenys* in the vivarium. British Jour. Herp., 2(12):217-218.
1963a. Notes on the eyed gecko *(Pachydactylus geitje)* with special reference to incubation. Copeia, 1963(2):433-434.
1963b. Growth, sloughing, feeding, mating, gestation, life span and poor health of chameleons in captivity. Copeia, 1963(4):704-706.
1963c. Sexual dichromatism in *Sceloporus cyanogenys*. Herpetologica, 19(2):149-150.
1964. Reproduction in the Australian rain forest skinks, *Siaphos equalis* and *Sphenomorphus tryoni*. Copeia, 1964:715-716.
1965a. The systematic status of the Australian geckos *Gehyra variegata* (Duméril and Bibron, 1836) and *Gehyra australis* Gray, 1845. Herpetologica, 20(4):259-272.
1965b. Observations on the life history and behavior of *Chamaeleo hohnelii* (Steindachner). Copeia, 1965(4):401-410.
1966. Observations on the life history and behavior of *Chamaeleo bitaeniatus* Fischer. Herpetologica, 22(1):13-23.
1967. Reproduction in an Australian gekkonid genus *Oedura* Gray 1842. Herpetologica, 23(4):276-284.
1968a. The reptiles of Merriwindi State Forest, Pilliga West, Northern New South Wales. Herpetologica, 24(2):131-140.
1968b. The eggshell of gekkonid lizards, a taxonomic adjunct. Copeia, 1968(1):162-164.
1968c. The ecology of the Australian gecko *Heteronotia binoei* in northern New South Wales. Jour. Zool., 156(4):483-497.
1969. The population ecology of the gekkonid lizard *Gehyra variegata* (Duméril and Bibron) in exploited forests in northern New South Wales. Jour. Animal Ecol., 38:35-51.

Cagle, F. R.
1937. Notes on Natrix rhombifera as observed at Reelfoot Lake. Jour. Tennessee Acad. Sci., 12:179-185.
1946a. A lizard population on Tinian. Copeia, 1946(1):4-9.
1946b. Eggs of the lizard *Gehyra oceanica*. Copeia, 1946(2):101.
1946c. *Typhlops braminus* in the Marianas Islands. Copeia, 1946:101.
1950. Notes on *Holbrookia texana* in Texas. Copeia, 1950(3):230.

Campbell, H., and R. S. Simmons
1961. Notes on the eggs and young of *Eumeces callicephalus* Bocourt. Herpetologica, 17(3):212-213.

Carpenter, C. C.
1952a. Comparative ecology of the common garter snake *(Thamnophis s. sirtalis)*, the ribbon snake *(Thamnophis s. sauritus)*, and Butler's garter snake *(Thamnophis butleri)* in mixed populations. Ecol. Monogr., 22(4):235-258.
1952b. Growth and maturity of the three species of *Thamnophis* in Michigan. Copeia, 1952(4):237-243.
1958. Reproduction, young, eggs and food of Oklahoma snakes. Herpetologica, 14(2):113-115.
1959a. A population of *Sceloporus undulatus consobrinus* in south-central Oklahoma. Southwestern Nat., 4(2):110.
1959b. A population of the six-lined racerunner *(Cnemidophorus sexlineatus)*. Herpetologica, 15(2):81-86.
1960a. Reproduction in Oklahoma *Sceloporus* and *Cnemidophorus*. Herpetologica, 16(3):175-182.
1960b. Parturition and behavior at birth of Yarrow's spiny lizard *(Sceloporus jarrovi)*. Herpetologica, 16(2):137-138.
1960c. A large brood of western pigmy rattlesnakes. Herpetologica, 16(2):142-143.

1966. The marine iguana of the Galapagos Islands, its behavior and ecology. Proc. Calif. Acad. Sci., Fourth Ser., 34(6):329-376.

Carr, A. F.
1940. A contribution to the herpetology of Florida. Univ. Florida Publ. Biol. Sci. Ser., 3(1):1-118.
1949. Notes on eggs and young of the lizard *Rhineura floridana*. Copeia, 1949(1):77.

Carson, H. L.
1945. Delayed fertilization in a captive indigo snake. Copeia, 1945(4): 222-225.

Chaney, A. H., and R. E. Gordon
1954. Notes on a population of *Sceloporus merriami* Stejneger. Texas Jour. Sci., 6(1):78-82.

Chapman, B. M., and R. F. Chapman
1964. Observations on the biology of the lizard *Agama agama* in Ghana. Proc. Zool. Soc. London, 143:121-132.

Chopra, R. N.
1964. Observations on the egg-laying of the fan-throated lizard, *Sitana ponticeriana* Cuv. Jour. Bombay Nat. Hist. Soc., 61(1):190-191.

Church, G.
1962. The reproductive cycles of the Javanese house geckos, *Cosymbotus platyurus*, *Hemidactylus frenatus*, and *Peropus mutilatus*. Copeia, 1962(2):262-269.

Clark, D. R., Jr.
1963. Variation and sexual dimorphism in a brood of the western pigmy rattlesnake (*Sistrurus*). Copeia, 1963(1):157-159.
1964. Reproduction and sexual dimorphism in a population of the rough earth snake, *Virginia striatula* (Linneaus). Texas Jour. Sci., (16)3: 265-295.
——. An ecological study of the worm snake, *Carphophis vermis* (Kennicott). Univ. Kansas Publ. Mus. Nat. Hist., 19(2), in press.

Clark, H.
1953. Eggs, egg-laying and incubation of the snake *Elaphe emoryi* (Baird and Girard). Copeia, 1953(2):90-92.

Clark, R. F.
1949. Snakes of the hill parishes of Louisiana. Jour. Tennessee Acad. Sci., 24(4):244-261.

Clarke, R. F.
1954. Eggs and egg-laying of *Lampropeltis c. calligaster* (Harlan). Herpetologica, 10:15-16.
1955. Observations on *Eumeces s. septentrionalis* in Kansas. Herpetologica, 11(3):161-164.

Clausen, H. J.
1936. Observations on the brown snake, *Storeria dekayi* (Holbrook), with especial reference to the habits and birth of young. Copeia, 1936(2):98-102.

Cogger, H.
1967. Australian reptiles in colour. East-West Center Press, Honolulu, 112 pp., 49 pls.

Cole, C. J.
1963. Variation, distribution, and taxonomic status of the lizard, *Sceloporus undulatus virgatus* Smith. Copeia, 1963(2):413-425.

Conant, R.
1934. Observations on the eggs and young of the black king snake, *Lampropeltis getulus nigra* (Yarrow). Copeia, 1934(4):188-189.
1938. On the seasonal occurrence of reptiles in Lucas County, Ohio. Herpetologica, 1(5):137-144.
1942. Notes on the young of three recently described snakes, with comments upon their relationships. Bull. Chicago Acad. Sci., 6(10): 193-200.
1951. The reptiles of Ohio. 2nd edition, Notre Dame, pp. 1-284.

1965 Notes on reproduction in two natricine snakes from Mexico. Herpetologica, 21(2):140-144.

Conant, R., and A. Downs, Jr.
1940. Miscellaneous notes on the eggs and young of reptiles. Zoologica, 25:33-48.

Condit, J. M.
1955. An albino milksnake, *Lampropeltis doliata triangulum,* from Ohio. Copeia, 1955(3):257.

Cook, F. R.
1964. Communal egg laying in the smooth green snake. Herpetologica, 20(3):206.

Cooper, J. S.
1958. Observations on the eggs and young of the wall lizard *(Lacerta muralis)* in captivity. British Jour. Herp., 2(7):112-121.

Cope, E. D.
1900. The crocodilians, lizards, and snakes of North America. Rept. U.S. Nat. Mus. for 1898, pp. 153-1270.

Cowles, R. B.
1935. Notes on the life history of *Pituophis catenifer deserticola* (Stejneger). Copeia, 1935(1):44.
1936. Casual notes on the poikilothermous vertebrates of the Umzumbe Valley, Natal, South Africa. Copeia, 1936(1):4-8.

Cowles, R. B., and C. M. Bogert
1944. A preliminary study of the thermal requirements of desert reptiles. Bull. Amer. Mus. Nat. Hist., 38:261-296.

Cuellar, O.
1966. Delayed fertilization in the lizard *Uta stansburiana.* Copeia, 1966 (3):549-552.

Cunningham, J. D.
1958. Alligator lizard notes. Herpetologica, 14(3):180.
1959. Reproduction and food of some California snakes. Herpetologica, 15(1):17-19.

Crenshaw, J. W., Jr.
1955. The life history of the southern spiny lizard, *Sceloporus undulatus undulatus* Latreille. Amer. Midl. Nat., 54(2):257-298.

Curtis, L.
1949a. Notes on the eggs of *Heloderma horridum.* Herpetologica, 5(6): 148.
1949b. The snakes of Dallas County, Texas. Field and Laboratory, 17(1): 5-13.

Dammann, J.
1949a. Notes on *Sceloporus undulatus tristichus* Cope. Herpetologica, 5 (6):143.
1949b. Birth of 18 young *Phrynosoma douglasii hernandesi* (Girard). Herpetologica, 5(6):144.

Daniel, P. M.
1960. Growth and cyclic behavior in the West African lizard *Agama agama africana.* Copeia, 1960(2):94-97.

Darevsky, I. S.
1960. Sezonnye izmeneniya zhirovykh tel i gonad u nekotorykh yashcherits doliny reki Araks v Armenii. Zool. Zhur., 39(8):1209-1217.

Darevsky, I. S., and S. Kadarson
1964. O biologii gigantskogo indoneziiskogo varana (*Varanus komodoensis* Ouwens). Zool. Inst. Acad. Sci., U.S.S.R., Leningrad.

Darevsky, I. S., and V. N. Kulikova
1962. Sistematicheskie priznaki i nekotorye osobennosti oogeneza gibridov mezhdu oboepoloi i partenogeneticheskoi formami skal'noi Yashcheritsy. Tsitologiya, 4(2):160-170.

Davis, W. B., and J. R. Dixon
1961. Reptiles (exclusive of snakes) of the Chilpancingo region, Mexico. Proc. Biol. Soc. Washington, 74:37-56.

Davis, W. B., and H. M. Smith
1953. Lizards and turtles of the Mexican state of Morelos. Herpetologica, 9(2):100-108.
DeHaas, C. P. J.
1941. Some notes on the biology of snakes and their distribution in two districts of west Java. Treubia, 18(2):327-375.
Denman, N. S., and I. S. Lapper
1964. The herpetology of Mont St.-Hilaire, Rouville County, Quebec, Canada. Herpetologica, 20(1):25-30.
Dietrich, S. E.
1960. Record clutch of *Lampropeltis* eggs. Herpetologica, 16(1):47.
Ditmars, R. L.
1936. The reptiles of North America. New York, pp. xvi + 476.
Dixon, J. R.
1964. The systematics and distribution of lizards of the genus *Phyllodactylus* in North and Central America. New Mexico State Univ. Res. Center, Sci. Bull. 64-1, 139 pp.
Dmi'el, R.
1967. Studies on reproduction, growth, and feeding in the snake *Spalerosophis cliffordi* (Colubridae). Copeia, 1967(2):332-346.
Donoso-Barros, R.
1966. Reptiles de Chile. Edición de la Universidad de Chile, Santiago, 458 pp., 111 pls.
Douglas, C. L.
1966. Amphibians and reptiles of Mesa Verde National Park, Colorado. Univ. Kansas Publ. Mus. Nat. Hist., 15(15):711-744.
Dowling, H. G.
1950. Studies of the black swamp snake, *Seminatrix pygaea* (Cope), with descriptions of two new subspecies. Misc. Publ. Mus. Zool. Univ. Michigan, No. 76, 38 pp.
Duellman, W. E.
1958. A monographic study of the colubrid snake genus *Leptodeira*. Bull. Amer. Mus. Nat. Hist., 114, article 1, 152 pp.
1961. The amphibians and reptiles of Michoacán, Mexico. Univ. Kansas Publ. Mus. Nat. Hist., 15(1):1-148.
1963. Amphibians and reptiles of the rainforests of southern El Petén, Guatemala. Univ. Kansas Publ. Mus. Nat. Hist., 15(5):205-249.
1965. Amphibians and reptiles from the Yucatán Peninsula, Mexico. Univ. Kansas Publ. Mus. Nat. Hist., 15(12):577-614.
Duellman, W. E., and A. S. Duellman
1959. Variation, distribution, and ecology of the iguanid lizard, *Enyaliosaurus clarki* of Michoacán, Mexico. Occas. Papers Mus. Zool. Univ. Michigan, No. 598:1-10.
Duellman, W. E., and A. Schwartz
1958. Amphibians and reptiles of southern Florida. Bull. Florida State Mus., 3(5):181-324.
Dunn, E. R.
1944. Herpetology of the Bogotá area. Revista de la Academia Colombiana de Ciencias Exactas, Físicas y Naturales, 6:68-81.
Echternacht, A. C.
1967. Ecological relationships of two species of the lizard genus *Cnemidophorus* in the Santa Rita Mountains of Arizona. Amer. Midl. Nat., 78:448-459.
Edgren, R. A.
1948. Notes on a litter of young timber rattlesnakes. Copeia, 1948(2):132.
Eibl-Eibesfeldt, I.
1961. Galapagos, the Noah's ark of the Pacific. (Translated from the German by Alan Houghton Brodrick.) Doubleday and Co., Inc., N.Y., 192 pp.
Erwin, D. B.
1964. Some findings on newborn rubber boas, *Charina b. bottae*. Copeia, 1964(1):222-223.

Evans, L. T.
1951. Field study of the social behavior of the black lizard, *Ctenosaura pectinata*. Amer. Mus. Novit., no. 1493:1-26.
1953. Tail display in an iguanid lizard, *Liocephalus carinatus coryi*. Copeia, 1953(1):50-54.

Fisher, E. M.
1925. Notes on the breeding of the California gopher snake in captivity. Copeia, No. 137:108-109.

Fitch, A. V.
1964. Temperature tolerances of embryonic *Eumeces*. Herpetologica, 20 (3):184-187.

Fitch, H. S.
1936. Amphibians and reptiles of the Rogue River basin, Oregon. Amer. Midl. Nat., 17(3):634-652.
1940a. A biogeographical study of the Ordinoides Artenkreis of garter snakes (genus Thamnophis). Univ. California Publ. Zool., 44:1-150.
1940b. A field study of growth and behavior in the fence lizard. Univ. Calif. Publ. Zool., 44:151-172.
1949. Study of snake populations in central California. Amer. Midl. Nat. 41(3):513-579.
1954. Life history and ecology of the five-lined skink, *Eumeces fasciatus*. Univ. Kansas Publ. Mus. Nat. Hist., 8(1):1-156.
1956. An ecological study of the collared lizard *(Crotaphytus collaris)*. Univ. Kansas Publ. Mus. Nat. Hist., 8(3):213-274.
1958. Natural history of the six-lined racerunner *(Cnemidophorus sexlineatus)*. Univ. Kansas Publ. Mus. Nat. Hist., 11(2):11-62.
1960. Autecology of the copperhead. Univ. Kansas Publ. Mus. Nat. Hist., 13(4):85-288.
1963. Natural history of the racer Coluber constrictor. Univ. Kansas Publ. Mus. Nat. Hist., 15(8):351-468.
1965. An ecological study of the garter snake, Thamnophis sirtalis. Univ. Kansas Publ. Mus. Nat. Hist., 15(10):493-564.

Fitch, H. S., and H. W. Greene
1965. Breeding cycle in the ground skink, Lygosoma laterale. Univ. Kansas Publ. Mus. Nat. Hist., 15(11):565-575.

FitzSimons, F. W.
1919. The snakes of South Africa. Capetown, pp. xvi + 550.

FitzSimons, V. F. M.
1943. The lizards of South Africa. Transvaal Museum Memoir No. 1, xv + 528.
1962. Snakes of southern Africa. Purnell and Sons, Ltd., Cape Town, 423 pp.

Flury, A.
1949. *Gerrhonotus liocephalus infernalis* Baird in Texas. Herpetologica, 5(3):65-67.

Force, E. R.
1930. The amphibians and reptiles of Tulsa County, Oklahoma. Copeia, 1930(2):25-39.
1931. Habits and birth of young of the lined snake, *Tropidoclonion lineatum* (Hallowell). Copeia, 1931(2):51-53.
1935. A local study of the opisthoglyph snake, *Tantilla gracilis* Baird and Girard. Papers Michigan Acad. Sci., Arts and Letters, 20:645-659.
1936. The relation of the knobbed anal keels to age and sex in the lined snake, *Tropidoclonion lineatum* (Hallowell). Papers Michigan Acad. Sci., Arts and Letters, 21:613-617.

Fouquette, M. J., and D. A. Rossman
1963. Noteworthy records of Mexican amphibians and reptiles in the Florida State Museum and Texas Natural History collection. Herpetologica, 19(3):185-201.

Fox, W., and H. C. Dessauer
1958a. Response of the male reproductive system of lizards *(Anolis carolinensis)* to unnatural day-lengths in different seasons. Biol. Bull., 115 (3):421-439.
1958b. Growth rates in captive male green anoles. Herpetologica, 14:196-197.
Fox, W., C. Gordon, and M. H. Fox
1961. Morphological effects of low temperatures during the embryonic development of the garter snake. Zoologica, 46(part 2):57-71.
Franklin, M. A.
1944. Notes on the young of the brown water snake. Copeia, 1944(4):250.
Fritts, T. H.
1966. Notes on the reproduction of *Xenosaurus grandis* (Squamata: Xenosauridae). Copeia, 1966(3):598.
Fuhn, I. E., and S. Vancea
1961. Fauna Republicii Populare Romine Reptilia. Editura Academisi Republicii Populaire Romine, vol. xiv, Fasc. 2, 349 pp.
Fukada, H.
1959. Growth and maturity of *Natrix tigrina tigrina* (Boie). Biological studies on the snakes. VI. Bull. Kyoto Gakugei Univ., Ser. B, (15): 25-41.
1960. Growth and maturity of *Elaphe quadrivirgata* (Boie). Biological studies on the snakes. VII. Bull. Kyoto Gakugei Univ., Ser. B, (16):6-21.
1962. Breeding habits of *Agkistrodon halys blomhoffii* (Boie). Biological studies on the snakes. IX. Bull. Kyoto Gakugei Univ., Ser. B, (20):12-17.
1963. Eggs and young of *Dinodon orientale* (Hilgendorf). Biological studies on the snakes. X. Bull. Kyoto Gakugei Univ., Ser. B, (22): 1-8.
1964. Eggs and young of *Trimeresurus okinavensis* Boulenger. Biological studies on the snakes. XI. Bull. Kyoto Gakugei Univ., Ser. B, (24):7-10.
1965. Breeding habits of some Japanese reptiles (critical review). Bull. Kyoto Gakugei Univ., Ser. B, (27):65-82.
Funk, R. S.
1964. On the reproduction of *Micruroides euryxanthus* (Kennicott). Copeia, 1964(1):219.
1966. Notes about *Heloderma suspectum* along the western extremity of its range. Herpetologica, 22(4):254-258.
Gaige, H. T.
1936. Some reptiles and amphibians from Yucatan and Campeche, Mexico. Carn. Inst. Wash., Publ. 454:289-304.
Gaige, H. T., N. Hartweg, and L. C. Stuart
1937. Notes on a collection of amphibians and reptiles from eastern Nicaragua. Occas. Papers Mus. Zool. Univ. Michigan, no. 357:1-3, 12-18.
Gander, F.
1931. Observations on an alligator lizard. Copeia, 1931(1):14-15.
Gans, C.
1964. Redescription of *Amphisbaena dubia* Müller (Amphisbaenia: Reptilia). Breviora, Mus. Comp. Zool., 205, 11 pp.
1967. A checklist of the recent amphisbaenids (Amphisbaenia: Reptilia). Amer. Mus. Nat. Hist. Bull., 135(2):61-106.
Gans, C., R. F. Laurent, and H. Pandit
1965. Notes on a herpetological collection from the Somali Republic. Mus. Royal Afrique Central, Tervuren Belgique Annales, Ser. 8, No. 134, 93 pp.
Gates, G. O.
1956. Mating habits of the Gila monster. Herpetologica, 12(3):184.
Gehlbach, F. R.
1965. Herpetology of the Zuni Mountains region, northwestern New Mexico. Proc. U.S. Nat. Mus., 116:243-322.

Gehlbach, F. R., and B. B. Collette
1959. Distributional and biological notes on the Nebraska herpetofauna. Herpetologica, 15(3):141-143.
Glissmeyer, H. R.
1951. Symposium: A snake den in Tooele County, Utah. Egg production of the Great Basin rattlesnake. Herpetologica, 7(1):24-27.
Gloyd, H. K.
1928. The amphibians and reptiles of Franklin County, Kansas. Trans. Kansas Acad. Sci., 31:115-141.
Gloyd, H. K., and R. Conant
1934. The taxonomic status, range, and natural history of Schott's racer. Occas. Papers Mus. Zool. Univ. Michigan, No. 287, 17 pp.
Goin, O. B., and C. J. Goin
1951. Notes on the natural history of the lizard, *Eumeces laticeps*, in northern Florida. Quart. Jour. Florida Acad. Sci., 14(1):29-33.
Grandison, A. G. C., and P. W. Soman
1963. Description of a new geckonid lizard from Maharashtra, India. Jour. Bombay Nat. Hist. Soc., 60(2):320-325.
Greene, H. W.
1969. Reproduction in a Middle American skink, *Leiolopisma cherriei* (Cope). Herpetologica, 25:55-56.
Greene, H. W., and B. E. Dial
1966. Brooding behavior by female Texas alligator lizards. Herpetologica, 22(4):303.
Greer, A. E.
1966. Viviparity and oviparity in the snake genera *Conopsis, Toluca, Gyalopion,* and *Ficimia,* with comments on *Tomodon* and *Helicops.* Copeia, 1966:371-373.
1967. Notes on the mode of reproduction in anguid lizards. Herpetologica, 23(2):94-99.
1968a. Mode of reproduction in the squamate faunas of three altitudinally correlated life zones in East Africa. Herpetologica, 24(3):229-232.
1968b. Clutch size in the scincid genus *Emoia.* Copeia, 1968(2):417-418.
1968c. The predominance of oviparity as a mode of reproduction in scincid lizards. Copeia, 1968(1):171.
Groves, F.
1960. The eggs and young of *Drymarchon corais couperi.* Copeia, 1960 (1):51-53.
Guidry, E. V.
1953. Herpetological notes from southeastern Texas. Herpetologica, 9(1): 49-56.
Hain, M. L.
1965. Ecology of the lizard *Uta mearnsi* in a desert canyon. Copeia, 1965(1):78-81.
Haines, T. P.
1940. Delayed fertilization in *Leptodeira annulata polysticta.* Copeia, 1940(2):116-118.
Hall, R. J.
1969. Ecological observations on Graham's water snake (*Regina grahami* Baird and Girard). Amer. Midl. Nat., 81(1):156-163.
Hallinan, T.
1920. Notes on lizards of the Canal Zone, Isthmus of Panama. Copeia, (83):45-49.
Hamilton, W. J., Jr., and J. A. Pollack
1958. Notes on the life history of the red-tailed skink. Herpetologica, 14(1):25-28.
Hamlett, G. W. D.
1952. Notes on breeding and reproduction in the lizard, *Anolis carolinensis.* Copeia, 1952(3):183-185.
Hanlon, R. W.
1964. Reproductive activity of the Bahaman boa. Herpetologica, 20(2): 143-144.

Harris, V. A.
1964. The life of the rainbow lizard. Hutchison Tropical Monographs. Hutchison and Co., Ltd., London, 174 pp.

Hebard, W. B.
1950. A dimorphic color pattern of the garter snake, *Thamnophis elegans vagrans* in the Puget Sound region. Copeia, 1950(3):217-219.
1951. Notes on the life history of the Puget Sound garter snake, *Thamnophis ordinoides*. Herpetologica, 7(4):177-179.

Hediger, H.
1934. Beitrag zur herpetologie und zoogeographie Neu Britanniens und einiger umliegender Gebiete. Zool. Jahrb., Bd. 65, Heft 516, pp. 441-582.

Herre, A. W. C. T., and D. S. Rabor
1949. Notes on Philippine sea snakes of the genus *Laticauda*. Copeia, 1949(4):282-284.

Hewatt, W. G.
1937. Courting and egg-laying habits of *Phrynosoma cornutum*. Copeia, 1937(4):234.

Hibbard, C. W.
1937. *Hypsiglena ochrorhynchus* in Kansas and additional notes on *Leptotyphlops dulcis*. Copeia, 1937(1):74.
1964. A brooding colony of the blind snake, *Leptotyphlops dulcis dissecta* Cope. Copeia, 1964(1):222.

Hickman, J. L.
1960. Observations on the skink lizard *Egernia whitii* (Lacépède). Papers and Proc. Royal Soc. Tasmania, 94:111-118.

Hirth, H. F.
1963a. The ecology of two lizards on a tropical beach. Ecol. Monogr., 33: 83-112.
1963b. Some aspects of the natural history of *Iguana iguana* on a tropical strand. Ecology, 44(3):613-615.
1964. Observations on the fer-de-lance, *Bothrops atrox*, in coastal Costa Rica. Copeia, 1964(2):453-454.

Hoddenbach, G. A.
1966. Reproduction in western Texas *Cnemidophorus sexlineatus* (Sauria, Teiidae). Copeia, 1966(1):110-113.

Hoddenbach, G. A., and J. R. Lannom, Jr.
1967. Notes on the natural history of the Mexican gecko, *Phyllodactylus tuberculosus*. Herpetologica, 23(4):293-296.

Hoddenbach, G. A., and F. B. Turner
1968. Clutch size of the lizard *Uta stansburiana* in southern Nevada. Amer. Midl. Nat., 80(1):262-265.

Holman, J. A.
1960. Reproduction in a pair of corn snakes, *Elaphe guttata guttata*. Copeia, 1960(3):239.

Hoover, E. E.
1936. On the birth of *Constrictor constrictor imperator* in captivity. Copeia, 1936(1):62.

Hopkins, J. R.
1968. The ecology and life history of *Sceloporus occidentalis longipes* Baird on Rainier Mesa at Nevada Test Site. MS

Hunsaker, D.
1959. Birth and litter sizes of the blue spiny lizard, *Sceloporus cyanogenys*. Copeia, 1959(3):260-261.

Inger, R. F., and B. Greenberg
1966. Annual reproductive patterns of lizards from a Bornean rain forest. Ecology, 47(6):1007-1021.

Irwin, L. N.
1965. Diel activity and social interaction of the lizard, *Uta stansburiana stejnegeri*. Copeia, 1965(1):99-101.

Isemonger, R. M.
1962. Snakes of Africa, southern, central and east. Thomas Nelson and Sons, Ltd., viii + 236 pp.
Johnson, C.
1960. Reproductive cycle in females of the greater earless lizard, *Holbrookia texana*. Copeia, 1960(4):299-300.
Johnson, D. H., M. D. Bryant, and A. H. Miller
1948. Vertebrate animals of the Providence Mountains area of California. Univ. California Publ. Zool., 48:221-376.
Johnson, R. M.
1953. A contribution on the life history of the lizard *Scincella laterale* (Say). Tulane Studies in Zoology, 1(2):11-27.
Johnson, S. R.
1965. An ecological study of the chuckwalla, *Sauromalus obesus* Baird, in the western Mojave Desert. Amer. Midl. Nat., 73(1):1-29.
Kassing, E. F.
1961. A life history study of the Great Plains ground snake, *Sonora episcopa episcopa* (Kennicott). Texas Jour. Sci., 13(2):185-203.
Kauffeld, C. F.
1943a. Field notes on some Arizona reptiles and amphibians. Amer. Midl. Nat., 29(2):342-359.
1943b. Growth and feeding of newborn Price's and green rock rattlesnakes. Amer. Midl. Nat., 29(3):607-614.
Kehl, R., and C. Combescot
1955. Reproduction in the Reptilia, pp. 57-74 *in* The comparative physiology of reproduction and the effects of sex hormones in vertebrates. Cambridge Univ. Press, x + 253 pp.
Kennedy, J. P.
1959. A minimum egg complement for the western mud snake, *Farancia abacura reinwardti*. Copeia, 1959(1):71.
1960. Parturition in the blue spiny lizard, *Sceloporus cyanogenys*. Southwestern Nat., 5(1):44-45.
1964. Natural history notes on some snakes of eastern Texas. Texas Jour. Sci., 16(2):210-215.
1965. Observations on the distribution and ecology of Barker's anole, *Anolis barkeri* Schmidt (Iguanidae). Zoologica, 50(1):41-46.
1968. Observations on the ecology and behavior of *Cnemidophorus guttatus* and *Cnemidophorus deppei* (Sauria, Teiidae) in southern Veracruz. Jour. Herp., 2(3-4):87-96.
In press A population study of the fence lizard, *Sceloporus undulatus*. Univ. Texas Press.
Khonyakina, Z. P.
1965. Biology of the Caucasian Agama of Dagestan, [in Russian] *in* Problems of physiology, biochemistry, zoology and parasitology. Makhachkala, 126-134.
Klauber, L. M.
1931. A statistical survey of the snakes of the southern border of California. Bull. Zool. Soc. San Diego, No. 8, 93 pp.
1933. Notes on *Lichanura*. Copeia, 1933(4):214.
1939a. Studies of reptile life in the arid Southwest. Bull. Zool. Soc. San Diego, No. 14, 100 pp.
1939b. A further study of pattern dimorphism in the California king snake. Bull. Zool. Soc. San Diego, No. 15, 23 pp.
1940a. The lyre snakes (genus *Trimorphodon*) of the United States. Trans. San Diego Soc. Nat. Hist., 9(19):163-194.
1940b. The worm snakes of the genus *Leptotyphlops* in the United States and northern Mexico. Trans. San Diego Soc. Nat. Hist., 9(18):87-162.
1941. The long-nosed snakes of the genus *Rhinocheilus*. Trans. San Diego Soc. Nat. Hist., 9(29):289-332.
1945. The geckos of the genus *Coleonyx* with descriptions of new subspecies. Trans. San Diego Soc. Nat. Hist., 10(11):133-216.

1946. The glossy snake, Arizona, with descriptions of new subspecies. Trans. San Diego Soc. Nat. Hist., 10(17):311-398.
1947. Classification and ranges of the gopher snakes of the genus Pituophis in the Western United States. Bull. Zool. Soc. San Diego, No. 22, 84 pp.
1956. Rattlesnakes their habits, life histories, and influence on mankind. Univ. California Press, xxix + 708 pp.

Kluge, A. G.
1967a. Higher taxonomic categories of gekkonid lizards and their evolution. Bull. Amer. Mus. Nat. Hist., 135(1):1-59.
1967b. Systematics, phylogeny, and zoogeography of the lizard genus *Diplodactylus* Gray (Gekkonidae). Australian Jour. Zool., 15:1007-1108.

Kluge, A. G., and M. J. Eckardt
1969. *Hemidactylus garnotii* Duméril and Bibron, a triploid all-female species of gekkonid lizard. Copeia, 1969(4):651-664.

Knepton, J. C.
1951. Reproduction by a king snake. Herpetologica, 7(2):85-89.

Kopstein, F.
1932. Herpetologische Notizen. VI. Weitere Beobachtungen über die Fortpflanzung west-javanischer Reptilien. Treubia, Buitenzorg, XIV:78-84.
1938. Ein Beitrag zur Eierkunde und zur Fortpflanzung der Malaiischen Reptilien. Bull. Raffles Mus., No. 14:81-167.

Kurfess, J. F.
1967. Mating, gestation, and growth in *Lichanura r. roseofusca.* Copeia, 1967(2):477-479.

Lardie, R. L.
1965. Eggs and young of *Rhinocheilus lecontei tessellatus.* Copeia, 1965 (3):366.

Lawson, R.
1952. Early breeding of the common lizard *(Lacerta vivipara).* British Jour. Herp., 1(7):133-134.

LeBuff, C. R., Jr.
1953. Observations on the eggs and young of *Drymarchon corais couperi.* Herpetologica, 9(4):166.

Leviton, A. E.
1963. Contributions to a review of Philippine snakes, II. The snakes of the genera *Liopeltis* and *Sibynophis.* Philippine Jour. Sci., 92(3): 367-381.
1965. Contributions to a review of Philippine snakes, VII. The snakes of the genera *Naja* and *Ophiophagus.* Philippine Jour. Sci., 93(4): 531-550.

Lewis, T. H.
1946. Notes on reptiles from the state of Washington. Copeia, 1946(3): 155-159.
1950. The herpetofauna of the Tularosa Basin and Organ Mountains of New Mexico with some notes on some ecological features of the Chihuahuan Desert. Herpetologica, 6(1):1-10.
1951. The biology of *Leiolopisma laterale* (Say). Amer. Midl. Nat., 45(1):232-240.

Licht, P., and W. R. Moberly
1965. Thermal requirements for embryonic development in the tropical lizard *Iguana iguana.* Copeia, 1965(4):515-517.

Lindberg, K.
1932. Snakes on the Barsi light railway (Deccan). Jour. Bombay Nat. Hist. Soc., 35:690-697.

Livezey, R. L., and R. S. Peckham
1953. Some snakes from San Marcos, Guatemala. Herpetologica, 8(4): 175-177.

Loomis, R. B.
1948. Notes on the herpetology of Adams County, Iowa. Herpetologica, 4(4):121-122.

Loveridge, A.
1929. East African reptiles and amphibians in the United States National Museum. U.S. Nat. Mus. Bull., 151, 135 pp.
1934. Australian reptiles in the Museum of Comparative Zoology, Cambridge, Massachusetts. Bull. Mus. Comp. Zool., 77(6):243-383.
1936. Scientific results of an expedition to rain forest regions in eastern Africa. Bull. Mus. Comp. Zool., 79(5):209-430.
1939. Revision of the African snakes of the genera *Mehelya* and *Gonionotophis*. Bull. Mus. Comp. Zool., 86(3):131-162.
1940. Revision of the African snakes of the genera *Dromophis* and *Psammophis*. Bull. Mus. Comp. Zool., 87(1):1-69.
1941. Revision of the African lizards of the family Amphisbaenidae. Bull. Mus. Comp. Zool., 87(5):353-451.
1942. Scientific results of a fourth expedition to forested areas in east and central Africa. Bull. Mus. Comp. Zool., 91(4):237-373.
1945. Reptiles of the Pacific World. The MacMillan Co., N.Y., xii + 259 pp.
1947. Revision of the African lizards of the family Gekkonidae. Bull. Mus. Comp. Zool., 98(1):469 pp.
1948. New Guinean reptiles and amphibians in the Museum of Comparative Zoology and the United States National Museum. Bull. Mus. Comp. Zool., 101(2):305-430.
1951. On reptiles and amphibians from Tanganyika Territory collected by C. J. P. Ionides. Bull. Mus. Comp. Zool., 106(4):177-204.
1953. Zoological results of a fifth expedition to East Africa. III. Reptiles from Nyasaland and Tete. Bull. Mus. Comp. Zool., 110(3):143-322.
1958. Revision of five African snake genera. Bull. Mus. Comp. Zool., 119 (1):1-198.

Lowe, C. H.
1942. Notes on the mating of desert rattlesnakes. Copeia, 1942(4):261-262.

Lowe, W.
1932. The trail that is always new. Gurney and Jackson, London, xviii + 271 pp.

Ludwig, M., and H. Rahn
1943. Sperm storage and copulatory adjustment in the prairie rattlesnake. Copeia, 1943:15-18.

Lynch, J. D.
1966. Communal egg laying in the pilot blacksnake, *Elaphe obsoleta obsoleta*. Herpetologica, 22(4):305.

MacMahon, J. A.
1957. Observations on mating in the corn snake, *Elaphe guttata guttata*. Copeia, 1957(3):232.

Maleev, E. A., and I. S. Darevsky
1963. "Drakony" ostrova Komodo. [Dragons from Komodo.] Priroda, 52 (3):24-35.

Malnate, E. V.
1960. Systematic division and evolution of the colubrid snake genus *Natrix* with comments on the subfamily Natricinae. Proc. Acad. Nat. Sci. Philadelphia, 112(3):41-71.
1962. The relationships of five species of the Asiatic natricine snake genus Amphiesma. Proc. Acad. Nat. Sci. Philadelphia, 114(8):251-299.

Malnate, E. V., and S. A. Minton
1965. A redescription of the natricine snake, *Xenochrophis cerasogaster*, with comments on its taxonomic position. Proc. Acad. Nat. Sci. Philadelphia, 117(2):19-43.

Malnate, E. V., and H. E. Munsterman
1960. Interpopulation variation in the colubrid snake *Natrix pryeri* from the Riukiu Islands, with a description of a new subspecies. Proc. California Acad. Sci., fourth ser., 31(2):51-67.

Manças, S.
1963. Sáurios de Angola. Memórias da Junta de Invevstigações do Ultramar. No. 43(2ª Série):225-240.

Marcy, D.
1945. Birth of a brood of *Crotalus basiliscus*. Copeia, 1945(3):169-170.

Marr, J. C.
1944. Notes on amphibians and reptiles from the central United States. Amer. Midl. Nat., 32:478-490.

Marshall, A. J., and R. Hook
1960. The breeding biology of equatorial vertebrates: reproduction of the lizard *Agama agama lionotus* Boulenger at Lat. 0° 01′ N. Proc. Zool. Soc. London, 134:197-205.

Marshall, F. H. A.
1956. Marshall's physiology of reproduction. (A. S. Parkes, editor.) Vol. 1, pt. 1, Longman's Green, London. (Third edition.)

Martin, P. S.
1958. A biogeography of reptiles and amphibians in the Gómez Farías region, Tamaulipas, Mexico. Misc. Publ. Mus. Zool., Univ. Michigan, No. 101, 102 pp.

Martof, B.
1954. Variation in a large litter of gartersnakes *Thamnophis sirtalis sirtalis*. Copeia, 1954(2):100-105.
1956. A contribution to the biology of the skink, *Eumeces laticeps*. Herpetologica, 12(2):111-114.

Maslin, T. P.
1947. Range extensions of three reptiles in Colorado. Copeia, 1947(2): 138.
1950. Snakes of the Kiukiang-Lushan area, Kiangsi, China. Proc. California Acad. Sci., 26, No. 12:419-466.
1963. Notes on a collection of herpetozoa from the Yucatan Peninsula of Mexico. Univ. of Colorado Studies, ser. in Biol. No. 9, pp. 1-20.

Mattlin, R. H.
1948. A large litter of *Thamnophis s. sirtalis*. Herpetologica, 4(4):149.

Mayhew, W. W.
1963. Reproduction in the granite spiny lizard, *Sceloporus orcutti*. Copeia, 1963(1):144-152.
1964a. Photoperiodic responses in three species of the lizard genus *Uma*. Herpetologica, 20(2):95-113.
1964b. Reproduction in the sand-dwelling lizard *Uma inornata*. Herpetologica, 21(1):39-55.
1966a. Reproduction in the psammophilous lizard *Uma scoparia*. Copeia, 1966(1):114-122.
1966b. Reproduction in the arenicolous lizard *Uma notata*. Ecology, 47 (1):9-18.

McCann, C.
1937a. Notes on the breeding of the rat-snake or dhaman *(Zamenis mucosus)*. Jour. Bombay Nat. Hist. Soc., 39:423-424.
1937b. Notes on *Calotes versicolor* (Daudin) Jerdon. Jour. Bombay Nat. Hist. Soc. 39:843-848.
1937c. Breeding season of the Jew's nosed seasnake [*Enhydrina valakadyen* Boie)] in Bombay waters. Jour. Bombay Nat. Hist. Soc., 39:872-873.
1940. A reptile and amphibian miscellany. Jour. Bombay Nat. Hist. Soc., 42:45-64.

McCauley, R. H., Jr.
1945. The reptiles of Maryland and the District of Columbia. Hagerstown, Maryland, ii + 194 pp.

McCoy, C. J., Jr.
1961. Birth season and young of *Crotalus scutulatus* and *Agkistrodon contortrix laticinctus*. Herpetologica, 17(2):140.
1967. Natural history notes on *Crotaphytus wislizeni* (Reptilia: Iguanidae) in Colorado. Amer. Midl. Nat., 77(1):138-147.
1968a. Reproductive cycles and viviparity in Guatemalan *Corythophanes percarinatus* (Reptilia: Iguanidae). Herpetologica, 24(2):175-178.
1968b. A review of the genus *Laemanctus* (Reptilia, Iguanidae). Copeia, 1968(4):665-678.
McCoy, C. J., Jr., and G. A. Hoddenbach
1966. Geographic variation in ovarian cycles and clutch size in *Cnemidophorus tigris* (Teiidae). Science, 154:1671-1672.
McGregor, R. C.
1904. Notes on Hawaiian reptiles from the Island of Maui. Proc. U.S. Nat. Mus., 28:115-118.
Meade, G. P.
1932. Notes on the breeding habits of Say's king snake in captivity. Bull. Antivenin Inst. Amer., 5(3):70-71.
1934. Some observations on captive snakes. Copeia, 1934(1):4-5.
1935. The egg-laying of *Farancia abacura*. Copeia, 1935(4):190-191.
1937. Breeding habits of *Farancia abacura* in captivity. Copeia, 1937(1):12-15.
Mendelssohn, H.
1963. On the biology of the venomous snakes of Israel. I., Israel Jour. Zool., 12(1/4):143-170.
1965. On the biology of the venomous snakes of Israel. II., Israel Jour. Zool., 14(1/4):185-212.
Mendietta, L.
1962. Dati sulla biologia del *Chalcides ocellatus*. Rend Inst. Sci. Univ. Camerino, 3(2-3):146-159.
Menzies, J. I.
1966. The snakes of Sierra Leone. Copeia, 1966(2):169-179.
Mertens, R.
1955. Die Amphibien und Reptilien Südwestafrikas. Aus den Ergebnissen einer im Jahre 1952 ausgefürten Reise. Abhand. Senckenbergischen Naturf. Gesell., 490, 172 pp.
Miller, C. M.
1944. Ecologic relations and adaptations of the limbless lizards of the genus *Anniella*. Ecol. Monogr., 14:271-289.
Miller, M. R.
1951. Some aspects of the life history of the yucca night lizard, *Xantusia vigilis*. Copeia, 1951(2):114-120.
1954. Further observations on reproduction in the lizard, *Xantusia vigilis*. Copeia, 1954(1):38-40.
1959. The endocrine basis for reproductive adaptations in reptiles. *In* Symposium of Comparative Endocrinology, A. Gorbman, ed. New York, Wiley and Sons.
Milstead, W. W.
1957. Observations on the natural history of four species of whiptail lizards, Cnemidophorus (Sauria, Teiidae), in Trans-Pecos Texas. Southwestern Nat., 2(2-3):105-121.
1961. Notes on teiid lizards in southern Brazil. Copeia, 1961(4):493-495.
Minton, S. A., Jr.
1944. Introduction to the study of reptiles of Indiana. Amer. Midl. Nat., 32:438-477.
1949. The black-headed snake in southern Indiana. Copeia, 1949(2):146-147.
1959. Observations on amphibians and reptiles of the Big Bend region of Texas. Southwestern Nat., 3:28-54.
1966. A contribution to the herpetology of West Pakistan. Bull. Amer. Mus. Nat. Hist., 134(2):31-184.

Mittleman, M. B.
1952. A generic synopsis of the lizards of the subfamily Lygosominae. Smithson. Misc. Coll., 117, no. 17, 35 pp.
Mole, R. H.
1924. The Trinidad snakes. Proc. Zool. Soc. London, no. 11, 1924:235-278.
Montanucci, R. R.
1965. Observations on the San Joaquin leopard lizard, *Crotaphytus wislizenii silus* Stejneger. Herpetologica, 21(4):270-283.
1967. Further studies on leopard lizards, *Crotaphytus wislizenii*. Herpetologica, 23(2):126.
Mosauer, W.
1932. The amphibians and reptiles of the Guadalupe Mountains of New Mexico and Texas. Occas. Papers Mus. Zool. Univ. Michigan, no. 246, 19 pp.
1934. The reptiles and amphibians of Tunisia. Publ. Univ. California at Los Angeles Biol. Sci., 1(3):49-64.
Mount, R. H.
1963. The natural history of the red-tailed skink, *Eumeces egregius* Baird. Amer. Midl. Nat., 70(2):356-385.
Mulaik, S.
1936. An ovoviviparous *Sceloporus* from Texas. Copeia, 1936(1):72.
Myers, C. W.
1965. Biology of the ringneck snake, *Diadophis punctatus*, in Florida. Bull. Florida State Mus., 10(2):43-90.
1967. The pine woods snake, *Rhadinea flavilata* (Cope). Bull. Florida State Mus., 11(2):47-97.
Myers, G. S.
1945. Nocturnal observations on sea-snakes in Bahia Honda, Panama. Herpetologica, 3(1):22-23.
Neill, W. T.
1951. Notes on the natural history of certain North American snakes. Publ. Res. Div. Ross Allen's Rept. Inst., 1(5):47-60.
1962. The reproductive cycle of snakes in a tropical region, British Honduras. Quart. Jour. Florida Acad. Sci., 25(3):234-253.
1964a. Taxonomy, natural history and zoogeography of the rainbow snake *Farancia erytrogramma* (Palisot de Beauvois). Amer. Midl. Nat., 71(2):257-295.
1964b. Viviparity in snakes: some ecological and zoogeographical considerations. Amer. Nat., 98(898):35-55.
Neill, W. T., and R. Allen
1959. Studies on the amphibians and reptiles of British Honduras. Publ. Res. Div. Ross Allen's Reptile Inst., 2(1):1-76.
1962. Parturient anaconda, *Eunectes gigas* Latreille, eating own abortive eggs and fetal membranes. Quart. Jour. Florida Acad. Sci., 25(1):73-75.
Neill, W. T., and J. L. Boyles
1957. The eggs of the crowned snake, *Tantilla coronata*. Herpetologica, 13(1):77-78.
Netting, M. G.
1936. Notes on a collection of reptiles from Barro Colorado Island, Panama Canal Zone. Ann. Carnegie Mus., 25:113-120.
New, J. G.
1953. The young of the snake, *Pituophis melanoleucus melanoleucus*. Copeia, 1953(3):182.
Noble, G. K.
1935. The brooding habits of the blood python and of other snakes. Copeia, 1935(1):1-3.
Norris, K. S.
1949. Observations on the habits of the horned lizard, *Phrynosoma m'callii*. Copeia, 1949(3):176-180.
1953. The ecology of the desert iguana *Dipsosaurus dorsalis*. Ecology, 34(2):265-287.

Ober, L. D.
1968. Reproduction and growth rate in the hispaniolan anguid *Diploglossus stenurus* Cope. Herpetologica, 24(4):326-327.
Oliver, J. A.
1947. The seasonal incidence of snakes. Am. Mus. Novit., No. 1363:1-14.
1956. Reproduction in the king cobra, *Ophiophagus hannah* Cantor. Zoologica, 41(4):145-152, 5 pls.
Oliver, J. A., and C. E. Shaw
1953. The amphibians and reptiles of the Hawaiian Islands. Zoologica, 38(2):65-95.
Orejas Miranda, B. R.
1966. The snake genus *Lystrophis* in Uruguay. Copeia, 1966(2):193-205.
Ortleb, E. P.
1965. Hatching of basilisk eggs. Herpetologica, 20(4):277-279.
Osorno, E.
1938. On the habits of *Leiocephalus ornatus trachycephalus*. Copeia, 1938(4):200.
Palmer, W. M.
1959. Two large egg clutches of the broad-headed skink, *Eumeces laticeps*. Herpetologica, 15(3):163.
Pandha, S. K., and J. P. Thapliyal
1967. Egg laying and development in the garden lizard, *Calotes versicolor*. Copeia, 1967(1):121-125.
Parker, M. V.
1948. A contribution to the herpetology of western Tennessee. Jour. Tennessee Acad. Sci., 22(1):20-30.
Pearson, O. P.
1954. Habits of the lizard *Liolaemus multiformis multiformis* at high altitudes in southern Perú. Copeia, 1954(2):111-116.
Perkins, C. B.
1943. Notes on captive-bred snakes. Copeia, 1943(2):108-112.
Peters, G.
1964. Sekundäre Geschlechtmerkmale, Wachstum und Fortpflanzung bei einigen transkaukasischen Eremias-Formen (Reptilia, Lacertidae). Senckenberg biol. 43(3/5):445-467.
Peterson, H. W.
1956. A record of viviparity in a normally oviparous snake. Herpetologica, 12(2):152.
Petzold, H.
1967. Some remarks on the breeding biology and the keeping of *Tretanorhinus variabilis*, a water snake of Cuba. Herpetologica, 23 (3):242-246.
Pienaar, U. de V.
1966. The reptile fauna of the Kruger National Park. Koedoe, 1966, no. 1, 223 pp.
Pimentel, R. A.
1959. Positive embryo-maternal size correlation in the northern alligator lizard, *Gerrhonotus coeruleus principis*. Herpetologica, 15(1):6-8.
Platt, D. R.
1969. Natural history of the eastern and western hognose snakes *Heterodon platyrhinos* and *Heterodon nasicus*. Univ. Kansas Publ. Mus. Nat. Hist., 18(4):253-420.
Pope, C. H.
1929. Notes on reptiles from Fukien and other Chinese provinces. Bull. Amer. Mus. Nat. Hist., 58:335-487.
1935. The reptiles of China, turtles, crocodilians, snakes, lizards. Natural history of Central Asia, vol. 10, xlii + 604 pp. Published by the American Museum of Natural History.
1944. Amphibians and reptiles of the Chicago area. Chicago Mus. Nat. Hist. Press, 275 pp.
1961. The giant snakes. Alfred Knopf, New York, 290 pp.

Quesnel, V. C.
1957. The life history of the streak gecko *Gonatodes vittatus* (Licht.). Jour. Trinidad Field Nat. Club, 1957:5-14.
Rahn, H.
1942. The reproductive cycle of the prairie rattler. Copeia, 1942(4): 233-240.
Ramsey, L. W.
1946. Captive specimens of *Tropidoclonion lineatum*. Herpetologica, 3 (4):112.
1953. The lined snake, *Tropidoclonion lineatum* (Hallowell). Herpetologica, 9(1):7-24.
1956. Nesting of the Texas horned lizard. Herpetologica, 12(3):239-240.
Rand, A. S.
1963. Notes on the *Chamaeleo bitaeniatus* complex. Bull. Mus. Comp. Zool., 130(1):3-29.
1968. A nesting aggregation of iguanas. Copeia, 1968(3):552-561.
Ream, C. H.
1965. Notes on the behavior and egg laying of *Corythophanes cristatus*. Herpetologica, 20(4):239-242.
Reynolds, F. A.
1943. Notes on the western glossy snake in captivity. Copeia, 1943(3): 196.
Reynolds, F. A., and A. N. Solberg
1942. Notes on the life history of the mud snake. Copeia, 1942(1):25-26.
Richmond, N. D.
1945. The habits of the rainbow snake in Virginia. Copeia, 1945(1):28-30.
1956. Autumn mating of the rough green snake. Herpetologica, 12(4): 325.
Riemer, W. J.
1957. The snake *Farancia abacura:* an attended nest. Herpetologica, 13: 31-32.
Robertson, I. A. D., B. M. Chapman, and R. F. Chapman
1962. Notes on some reptiles collected in the Rukwa Valley, S. W. Tanganyika. Ann. Mag. Nat. Hist., 13(5):421-432.
1964. Notes on the biology of the lizards *Agama cyanogaster* and *Mabuya striata striata* in the Rukwa Valley, Southwest Tanganyika. Proc. Zool. Soc. London, 145:305-320.
Robison, W. G., Jr., and W. W. Tanner
1962. A comparative study of the species of the genus *Crotaphytus* Holbrook (Iguanidae). Brigham Young Univ. Sci. Bull., Biol. Ser., 2(1):1-31.
Rokosky, E. J.
1941. Notes on new-born jumping vipers, *Bothrops nummifera*. Copeia, 1941(4):267.
Rollinat, R.
1897. Moeurs et reproduction du lézard des murailles. Bull. Soc. Nat. d'Acclimatation de France, July 1897, 23 pp.
1900. Moeurs et reproduction du lézard vert. Mem. Soc. Zool. France, 13:5-30.
1934. La vie des reptiles de la France Centrale. Libr. Delagrave, Paris, 343 pp.
Rose, W.
1929. Veld and vlei, an account of South African frogs, toads, lizards, snakes and tortoises. The Specialty Press of South Africa, Ltd., Cape Town, xxiii + 240 pp.
Rossman, D. A.
1963. Relationships and taxonomic status of the North American natricine genera *Liodytes*, *Regina* and *Clonophis*. Occas. Papers Mus. Zool., Louisiana State Univ., no. 29, 29 pp.
Rossman, D. A., and R. M. Blaney
1968. A new natricine snake of the genus *Adelophis* from western Mexico. Occas. Papers Mus. Zool., no. 35, 12 pp.

Rossman, D. A., and L. D. Wilson
1964. Comments on the revival of the snake subfamily Heterodontinae. Herpetologica, 20(4):284-285.
Sabath, M., and R. Worthington
1959. Eggs and young of certain Texas reptiles. Herpetologica, 15(1): 31-32.
Saint-Girons, H.
1957. Le cycle sexuel chez *Vipera aspis* dans l'ouest de la France. Bull. Biol., 91:284-350.
1964. Notes sur l'écologie et la structure des populations des Laticaudinae (Serpents, Hydrophidae) en Nouvelle Caledonie. Terre Vie, 111 (2):185-214.
Saint-Girons, H., and E. Kramer
1963. Le cycle sexuel chez Vipera berus (L.) en montagne. Rev. Suisse Zool., 70(1):191-221.
Santos, E.
1955. Anfíbios e Répteis do Brasil. 2nd ed., F. Briguiet and Cia. Rio de Janeiro, 262 pp.
Sanyal, M. K., and M. R. N. Prasad
1967. Reproductive cycle of the Indian house lizard, *Hemidactylus flaviviridis* Rüppell. Copeia, 1967(3):627-633.
Sayer, P.
1953. Breeding of the green lizard *(Lacerta viridis)* in England. British Jour. Herp., 1(8):148-149.
Schmidt, K. P.
1923. Contributions to the herpetology of the Belgian Congo based on the collection of the American Museum Congo Expedition, 1909-1915. Part II, Snakes. Bull. Amer. Mus. Nat. Hist., 54:1-146.
Schmidt, K. P., and R. F. Inger
1957. Living reptiles of the world. Hanover House, Garden City, N.Y., 287 pp.
Schonberger, C. F.
1945. Oviposition by *Phrynosoma solare*. Copeia, 1945(1):53-54.
Seibert, H. C., and C. W. Hagen, Jr.
1947. Studies on a population of snakes in Illinois. Copeia, 1947(1):6-22.
Selander, R. K., R. F. Johnston, B. J. Wilks, and G. G. Raun
1962. Vertebrates from the barrier islands of Tamaulipas, Mexico. Univ. Kansas Publ. Mus. Nat. Hist., 12(7):309-345.
Sexton, O. J., and H. F. Heatwole
1965. Life history notes on some Panamanian snakes. Caribbean Jour. Sci., 5, nos. 1 and 2:39-43.
Sexton, O. J., H. F. Heatwole, and E. H. Meseth
1963. Seasonal population changes in the lizard, Anolis limifrons, in Panama. Amer. Midl. Nat., 69(2):482-491.
Shannon, F. A., and F. L. Humphrey
1963. Analysis of color pattern polymorphism in the snake, *Rhinocheilus lecontei*. Herpetologica, 19(3):153-160.
Shaw, C. E.
1943. Hatching of the eggs of the San Diego alligator lizard. Copeia, 1943(3):194.
1952. Notes on the eggs and young of some United States and Mexican lizards, I. Herpetologica, 8(3):71-79.
1954. Captive-bred cuban iguanas *Cyclura macleayi macleayi*. Herpetologica, 10(2):73-78.
1960. Notes on the eggs, incubation and young of *Chameleo basiliscus*. British Jour. Herp., 2(10):182-185.
1966. The eggs and young of the marine iguana *(Amblyrhynchus cristatus)*. Copeia, 1966(3):585.
Shoop, R.
1957. Eggs and young of the prairie king snake, *Lampropeltis c. calligaster*. Copeia, 1957(1):48-49.

Skinner, R. V.
1957. Observations on the smooth snake *(Coronella austriaca)* in East Dorset during the three years 1954-56. British Jour. Herp., 2(5): 94.
Slack, K. V.
1944. Notes on the egg laying of a black chicken snake. Copeia, 1944 (3):190-191.
Slevin, J. R.
1951. A high birth rate for *Natrix sipedon sipedon* (Linné). Herpetologica, 7(3):132.
Smith, C.
1941. Birth of horned toads. Copeia, 1941(2):114.
Smith, H. M.
1935. Miscellaneous notes on Mexican lizards. Univ. Kansas Sci. Bull., 22(6):119-155.
1936. The lizards of the Torquatus Group of the genus *Sceloporus* Wiegmann, 1828. Univ. Kansas Sci. Bull., 24(21):539-693.
1939. The Mexican and Central American lizards of the genus *Sceloporus*. Zool. Ser., Field Mus. Nat. Hist., 26:1-397.
1946. Handbook of lizards. Comstock Publ. Co., Inc., Ithaca, N.Y., 557 pp.
1949. Miscellaneous notes on Mexican lizards. Jour. Washington Acad. Sci., 39(1):34-43.
1963. Revival of Bonaparte's subfamily Heterodontinae of colubrid snakes. Herpetologica, 19(4):288-291.
Smith, H. M., and M. Alvarez del Toro
1963. Notulae herpetologicae Chiapasiae IV. Herpetologica, 19(2):100-105.
Smith, H. M., and H. W. Kerster
1955. New and noteworthy Mexican lizards of the genus *Anolis*. Herpetologica, 11(3):193-201.
Smith, H. M., and L. E. Laufe
1945. Mexican amphibians and reptiles in the Texas Cooperative Wildlife collections. Trans. Kansas Acad. Sci., 48(3):325-354.
Smith, H. M., and J. D. Lynch
1967. A new cryptic lizard (Iguanidae: *Sceloporus*) with comments on other reptiles from Oaxaca, Mexico. Herpetologica, 23(1):18-29.
Smith, H. M., T. P. Maslin, and R. L. Brown
1965. Summary of the distribution of the herpetofauna of Colorado. Univ. Colorado Studies, Series in Biol., No. 15, 52 pp.
Smith, H. M., and K. L. Williams
1953. New and noteworthy amphibians and reptiles from southern Mexico. Herpetologica, 19(1):22-27.
Smith, H. M., K. L. Williams, and E. O. Moll
1963. Herpetological explorations on the Rio Conchas, Chihuahua, Mexico. Herpetologica, 19(3):205-215.
Smith, M. A.
1935. The fauna of British India. Reptilia and Amphibia. Vol. II—Sauria, xiii + 440 pp.
1943. The fauna of British India. Reptilia and Amphibia. Vol. III—Serpentes, xii + 583 pp.
1951. The British amphibians and reptiles. Collins, London, xiv + 318 pp.
Smith, P. W.
1961. The amphibians and reptiles of Illinois. Bull. Illinois Nat. Hist. Surv., 28(1):1-298.
Smith, P. W., and W. L. Burger
1950. Herpetological results of the University of Illinois field expedition, spring 1949. III. Sauria. Trans. Kansas Acad. Sci., 53(2):165-175.
Smith, P. W., and J. C. List
1955. Notes on Mississippi amphibians and reptiles. Amer. Midl. Nat., 53(1):115-125.

Smith, P. W., H. M. Smith, and J. E. Werler
1952. Notes on a collection of amphibians and reptiles from eastern Mexico. Texas Jour. Sci., 1952(2):251-260.
Smith, R. E.
1968. Studies on reproduction in Costa Rican *Ameiva festiva* and *Ameiva quadrilineata* (Sauria: Teiidae). Copeia, 1968:236-239.
Smyth, M., and M. J. Smith
1968. Obligatory sperm storage in the skink *Hemiergis peronii*. Science, 161(3841):575-576.
Sowerby, A. C.
1914. The reptiles of North China, Manchuria and Mongolia, pp. 161-167 *in* Fur and feather in North China. Tientsin Press, Ltd., Tientsin.
Staedeli, J. H.
1964. Eggs and young of the vermillion-lined ground snake *Sonora semiannulata linearis*. Copeia, 1964:581-582.
Stebbins, R. C.
1954. Amphibians and reptiles of Western North America. McGraw-Hill Book Co., Inc., New York, xi + 528 pp.
1958. A new alligator lizard from the Panamint Mountains, Inyo County, California. Amer. Mus. Novit., No. 1883, 27 pp.
Stebbins, R. C., J. M. Lowenstein, and N. W. Cohen
1967. A field study of the lava lizard *(Tropidurus albemarlensis)* in the Galápagos Islands. Ecology, 48(5):839-851.
Stille, W. T.
1954. Observations on the reproduction and distribution of the green snake, *Opheodrys vernalis* (Harlan). Nat. Hist. Misc. Chicago Acad. Sci., no. 127:1-11.
Stuart, L. C.
1935. A contribution to a knowledge of the herpetology of a portion of the savanna region of central Petén, Guatemala. Univ. Michigan Misc. Publ., 29, 56 pp.
1942. Comments on several species of *Anolis* from Guatemala, with descriptions of three new forms. Univ. Michigan Occas. Papers Mus. Zool. No. 464, 10 pp.
1948. The amphibians and reptiles of Alta Verapaz, Guatemala. Misc. Publ. Mus. Zool. Univ. Michigan, No. 69, 109 pp.
1951. The herpetofauna of the Guatemalan Plateau, with special reference to its distribution on the southwestern highlands. Contrib. Lab. Vert. Biol., Univ. Michigan, No. 49, 71 pp.
1954. Herpetofauna of the southeastern highlands of Guatemala. Contr. Lab. Vert. Biol., Univ. Michigan, No. 68, 66 p.
1958. A study of the herpetofauna of the Uaxactún-Tikal area of northern el Petén, Guatemala. Contr. Lab. Vert. Biol., Univ. Michigan, No. 75, 30 pp.
Svihla, A.
1942. Mating behavior of the northern alligator lizard. Copeia, 1942(1): 54.
1943. Notes on young rubber snakes. Copeia, 1943(2):128.
Swanson, P. L.
1945. Herpetological notes from Panama. Copeia, 1945(4):210-216.
1948. *Natrix sipedon compressicauda* at Key West, Florida. Herpetologica, 4(3):105-106.
1950. The iguana *Iguana iguana iguana* (L). Herpetologica, 6:187-193.
Tanner, V. M.
1942. Notes on the birth and growth of horned lizards. Great Basin Nat., 3(2):60.
Tanner, V. M., and W. W. Tanner
1939. Notes on *Charina bottae* in Utah: reproduction. Great Basin Nat., 1:27-30.
Tanner, W. W.
1943. Notes on the life history of *Eumeces skiltonianus skiltonianus*. Great Basin Nat., 4(3-4):81-88.

1954. Herpetological notes concerning some reptiles of Utah and Arizona. Herpetologica, 10(2):92-96.
1957. A taxonomic and ecological study of the western skink *(Eumeces skiltonianus)*. Great Basin Nat., 17(3-4):59-94.
1958. Two new skinks from Durango, Mexico. Great Basin Nat., 18(2): 57-62.

Tanner, W. W., and C. D. Jorgensen
1963. Reptiles of the Nevada Test Site. Brigham Young Univ. Sci. Bull., Biol. Ser., 3(3):1-31.

Tanner, W. W., and W. G. Robison, Jr.
1960. Herpetological notes for northwestern Jalisco, Mexico. Herpetologica, 16(1):59-62.

Taub, A. M.
1963. On the longevity and fecundity of *Heloderma horridum horridum*. Herpetologica, 19(2):149.

Taylor, E. H.
1936. Notes on the herpetological fauna of the Mexican state of Sonora. Univ. Kansas Sci. Bull., 24(19):475-503.
1949. A preliminary account of the herpetology of the state of San Luis Potosí, Mexico. Univ. Kansas Sci. Bull., 33, pt. 1, no. 2:169-215.
1951a. A brief review of the snakes of Costa Rica. Univ. Kansas Sci. Bull., 34, pt. 1(1):188 pp.
1951b. Egg-laying behavior of an Oriental agamid lizard. Herpetologica, 7(2):59-60.
1956. A review of the lizards of Costa Rica. Univ. Kansas Sci. Bull., 38, Pt. 1(1):322 pp.
1963. The lizards of Thailand. Univ. Kansas Sci. Bul., 44(14):687-1077.
1965. The serpents of Thailand and adjacent waters. Univ. Kansas Sci. Bull., 45(9):609-1096.

Taylor, E. H., and R. E. Elbel
1958. Contribution to the herpetology of Thailand. Univ. Kansas Sci. Bull., 38, pt. 2(13):1033-1189.

Telford, S. R.
1955. A description of the eggs of the coral snake, *Micrurus f. fulvius*. Copeia, 1955(3):258.
1959. A study of the sand skink, *Neoseps reynoldsi* Stejneger. Copeia, 1959(2):110-119.
1969. The ovarian cycle, reproductive potential, and structure in a population of the Japanese lacertid *Takydromus tachydromoides*. Copeia, 1969(3):548-567.

Test, F. H., O. J. Sexton, and H. Heatwole
1966. Reptiles of Rancho Grande and vicinity, Estado Aragua, Venezuela. Misc. Publ. Mus. Zool., Univ. Michigan, No. 128, 63 pp.

Thien, J. A.
1949. A review of the lizard genus *Barisia*. Univ. Kansas Sci. Bull. 33, pt. 1, no. 3:217-256.

Tinkle, D. W.
1957. Ecology, maturation and reproduction of *Thamnophis sauritus proximus*. Ecology, 38(1):69-77.
1959. Observations on the lizards *Cnemidophorus tigris*, *Cnemidophorus tessellatus* and *Crotaphytus wislizenii*. Southwestern Nat., 4(4): 195-200.
1960. A population of *Opheodrys aestivus* (Reptilia: Squamata). Copeia, 1960(1):29-34.
1961. Population structure and reproduction in the lizard *Uta stansburiana stejnegeri*. Amer. Midl. Nat., 66(1):206-234.
1962. Reproductive potential and cycles in female *Crotalus atrox* from northwestern Texas. Copeia, 1962(2):306-313.

Tobiasz, E. C.
1941. Birth of two broods of massasaugas. Copeia, 1941(4):269.

Trapido, H.
1939. Parturition in the timber rattlesnake, *Crotalus horridus horridus* Linné. Copeia, (4):230.
1940. Mating time and sperm viability in *Storeria*. Copeia, 1940(2):107-109.

Triplehorn, C. A.
1955. Notes on the young of some North American reptiles. Copeia, 1955(3):248-249.

Tschambers, B.
1949. Birth of the Australian blue-tongued lizard, *Tiliqua scincoides* (Shaw). Herpetologica, 5(6):141-142.

Turner, F. B., J. R. Lannom, Jr., P. A. Medica, and G. A. Hoddenbach
1969. Density and composition of fenced populations of leopard lizards *(Crotaphytus wislizenii)* in southern Nevada. Herpetologica, 25(4): 247-256.

Underwood, G.
1967. A contribution to the classification of snakes. British Mus. (Nat. Hist.) London, 179 pp.

Uzzell, T. M., Jr.
1965. Teiid lizards of the genus *Echinosaura*. Copeia, 1965(1):82-89.
1966. Teiid lizards of the genus *Neusticurus* (Reptilia, Sauria). Bull. Amer. Mus. Nat. Hist., 132(5):279-327.

Vainio, I.
1931. Zur verbreitung und biologie der Kreuzotter, Vipera berus (L) in Finnland. Annales Societatis Zoolog-Botanicae Fennicae Vanamo, 12(1):1-19.

Valdivieso, D., and J. R. Tamsitt
1963. Records and observations on Colombian reptiles. Herpetologica, 19(1):28-39.

Vancea, S., and I. E. Fuhn
1959. Contributions à la systématique et à l'écologie des lacertides de la R. P. R. II. Le lézard vert des bois—*Lacerta viridis viridis* Laurentus. Analele Stiintifice ale Universitatii, Al. I Cuza din Iasi (serie Noua). Sectuina II, 5:61-80, 3 pls.

Van Denburgh, J.
1922. The reptiles of Western North America. Occas. Papers Calif. Acad. Sci., 10:1-1028.

Van Hyning, O. C.
1931. Reproduction of some Florida snakes. Copeia, (2):59-60.

Vanzolini, P. R.
1953. Sobre a diferenciação geografica de *Gymnodactylus geckoides* (Sauria, Gekkonidae). Pap. avulsos do dep. de Zool., 9(15):263-270.

Vestal, E. H.
1940. Mating posture in the alligator lizard *(Gerrhonotus coeruleus)*. Copeia, 1940(1):51.

Visser, J.
1967. Color varieties, brood size, and food of South African *Pelamis platurus* (Ophidia: Hydrophiidae). Copeia, 1967(1):219.

Volsoe, H.
1939. The sea snakes of the Iranian Gulf and the Gulf of Oman. Danish Sci. Invest. in Iran, Part 1.
1944. Structure and seasonal variation of the male reproductive organs of *Vipera berus* (L). Spolia Zool. Mus. Hauniensis, 5:1-157.
1956. Herpetology of Rennell Island. The Natural History of Rennell Island, British Solomon Islands. Vol. 1:121-134.

Waite, E. R.
1929. The reptiles and amphibians of South Australia. Govt. Printer, Adelaide, 270 pp.

Wall, F.
1905-1919. A popular treatise on the common Indian snakes. Jour. Bombay Nat. Hist. Soc., Part 1, 1905, 16:533-554 (*Lachesis gramineus, Dryophis mycterizans*).
Part 3, 1906, 17:259-272 (*Zamenis mucosus*).
Part 4, 1907, 17:857-869 (*Tropidonotus piscator*).
Part 5, 1907, 18:1-17 (*Vipera russellii*).
Part 7, 1907, 18:525-554 (*Dipsadomorphus trigonatus*).
Part 8, 1908, 18:711-735 (*Bungarus coeruleus*).
Part 9, 1909, 19:87-106 (*Lycodon aulicus*).
Part 13, 1910, 20:65-79 (*Psammodynastes pulverulentus*).
Part 14, 1911, 20:603-633 (*Tropidonotus stolatus*).
Part 16, 1911, 21:1-10 (*Eryx conicus*).
Part 17, 1912, 21:447-475 (*Python molurus*).
Part 18, 1912, 21:1009-1021 (*Helicops schistosus*).
Part 23, 1914, 23:34-43 (*Zamenis ventrimaculatus*).
Part 25, 1918, 25:375-382 (*Typhlops braminus, T. diardi*).
Part 25, 1918, 25:628-635 (*Silybura ocellata*).
Part 26, 1918, 26:89-97 (*Enhydris curtus, Cerberus rhynchops*).
1921. Ophidia Taprobanica or the snakes of Ceylon. H. R. Cottle, Govt. Printer, Colombo, xxii + 581 pp.

Webb, R. G.
1958. The status of the Mexican lizards of the genus *Mabuya*. Univ. Kansas Sci. Bull. 38, pt. 2(17):1303-1313.

Webb, R. G., J. K. Jones, Jr., and G. W. Byers
1962. Some reptiles and amphibians from Korea. Univ. Kansas Publ. Mus. Nat. Hist., 15(2):149-173.

Weekes, H. C.
1935. A review of placentation among reptiles with particular regard to the function and evolution of the placenta. Proc. Zool. Soc. London, Part 3:625-645.

Werler, J. E.
1949a. Reproduction of captive Texas and Mexican lizards. Herpetologica, 5(3):67-70.
1949b. Eggs and young of several Texas and Mexican snakes. Herpetologica, 5(2):59-60.
1951. Miscellaneous notes on the eggs and young of Texan and Mexican reptiles. Zoologica, 36(1):37-48, 7 pls.

Wharton, C. H.
1966. Reproduction in the cottonmouths, *Agkistrodon piscivorus* Lacépède, of Cedar Keys, Florida. Copeia, 1966:149-161.

White, M. E.
1957. The hatching and rearing of green lizards (*Lacerta viridis*). British Jour. Herp., 2(5):88-90.

Wilhoft, D. C.
1963. Reproduction in the tropical Australian skink, *Leiolopisma rhomboidalis*. Amer. Midl. Nat., 70(2):442-461.

Wilhoft, D. C., and E. O. Reiter
1965. Sexual cycle of the lizard, *Leiolopisma fuscum*, a tropical Australian skink. Jour. Morph., 116(3):379-387.

Wilson, D.
1959. The hatching and rearing of the cobra (*Naja melanoleuca*). British Jour. Herp., 2(9):159-162.

Wood, J. T.
1949. Observations on *Natrix septemvittata* (Say) in southwestern Ohio. Amer. Midl. Nat., 42(3):744-750.

Wood, S. F.
1936. Oviposition and embryos of some western lizards. Copeia, 1936 (1):69-70.

Woodin, W. H.
1950. Notes on Arizona species of *Thamnophis*. Herpetologica, 6(2): 39-40.

1953. Notes on some reptiles from the Huachuca area of southeastern Arizona. Bull. Chicago Acad. Sci., 9(15):285-296.

Woodward, S. F.

1933. A few notes on the persistence of active spermatozoa in the African night-adder, *Causus rhombeatus*. Proc. London Zool. Soc., 1933: 189-190.

Woolcott, W. S.

1959. Notes on the eggs and young of the scarlet snake, *Cemophora coccinea*. Blumenbach. Copeia, 1959(3):263.

Worrell, E.

1964. Reptiles of Australia. Angus and Robertson, xv + 207 pp.

Wright, A. H., and S. C. Bishop

1915. A biological reconnaissance of the Okefinokee Swamp in Georgia: II. Snakes. Proc. Acad. Nat. Sci. Philadelphia, 67:139-192.

Wright, A. H., and A. A. Wright

1957. Handbook of snakes of the United States and Canada. Comstock Publ. Associates, Cornell Univ. Press, vol. 1, xviii + 564 pp.; vol. 2, ix + 565-1105 pp.

Zehr, D. R.

1962. Stages in the normal development of the common garter snake, *Thamnophis sirtalis sirtalis*. Copeia, 1962(2):322-329.

Zweifel, R. G.

1949. Ovoviviparity in *Sceloporus jarrovii jarrovii*. Herpetologica, 5(6): 152.

1959. Variation in and distribution of lizards of western Mexico related to *Cnemidophorus sacki*. Bull. Amer. Mus. Nat. Hist., 117, art. 2: 63-116.

1962. Notes on the distribution and reproduction of the lizard *Eumeces callicephalus*. Herpetologica, 18(1):63-65.

Zweifel, R. G., and K. S. Norris

1955. Contribution to the herpetology of Sonora, Mexico: descriptions of new subspecies of snakes (Micrurcoides euryxanthus and Lampropeltis getulus) and miscellaneous collecting notes. Amer. Midl. Nat., 54:230-249.

3 2044 093 361 608

Date Due